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THE BOTTOM FAUNA OF LAKE SIMCOE AND ITS ROLE IN THE ECOLOGY OF THE LAKE

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INTRODUCTION

A complete study of the bottom fauna and its interrelations is necessary to a fuller understanding of the ecology of a lake and to an appreciation of its fisheries problems. It was with this in mind that an investigation of Lake Simcoe was begun in 1926 and was carried on during 1926-28. The present paper embodies the results of this study, dealing with the quantitative and qualitative aspects of the bottom fauna with special reference to its ecological relations.

In the original plan the investigation was to include a general biological survey of the lake in which the writer's part was to be a study of the bottom fauna. As a result, the work was organized on a somewhat different basis than if it had been proposed as a study in itself. After the first season it was found that the general survey could not be continued and it was therefore necessary in the second and third summers to devote considerable time to the collection of sufficient physico-chemical, plankton and fisheries data with which to interpret the results of the bottom fauna studies.

Lake Simcoe is of particular interest because it is intermediate in size between Lake Nipigon and the smaller American lakes in which the bottom fauna has been investigated. As a result of its intermediate size the life conditions are also intermediate and the ecological relations exemplified in Lake Simcoe aid in an interpretation of these other lakes.

The investigation of Lake Nipigon was undertaken in 1921 by the Ontario Fisheries Research Laboratory. This lake was a type of large lake, in a young, rocky country with its fisheries in an almost virgin condition. Lake Simcoe, on

the other hand, is a lake of intermediate size in a sedimentary region and with its fisheries somewhat depleted. Fishing in Lake Simcoe has included game fishing and some commercial fishing, a situation which has resulted in considerable difficulty in the fish cultural policy, a difficulty which is added to by the unusual fishing methods employed in the lake.

A preliminary report published in this series (Rawson, 1928) deals with the result of the first season's work. It is largely superseded by the present account which is more complete in all respects.

The investigation has been made possible by the supervision of members of the Ontario Fisheries Research Laboratory and others of the staff of the Department of Biology in the University of Toronto. Special thanks are due to Professors B. A. Bensley and W. J. K. Harkness for their kind assistance. In the early part of the work the writer was fortunate in having financial assistance from and the co-operation of the Biological staff of the Ontario Department of Game and Fisheries. Further thanks are due to the National Research Council for financial aid, to the Provincial Board of Health for certain chemical analyses and to specialists who identified certain of the organisms collected in the lake.

History of Bottom Fauna Investigation

Fresh-water biology as a definite study had its inception not more than fifty years ago. Marine biology was by this time well advanced, as instanced by the historic Challenger expedition of 1872-76, and it is well known that in its early development the fresh-water study received considerable inspiration from this source.

Of the various branches of limnobiology, the plankton was first to achieve prominence, chiefly through the works of Zacharias and Apstein, published in 1896. Early interest in the bottom inhabitants of lakes was aroused by Zschokke, Van Hofsten and Ekman, who studied the fauna from the depths of sub-alpine and Scandinavian lakes. Their interests were chiefly taxonomic and distributional, leading them into

the history of animal geography and especially the study of marine relicts.

In 1911, Ekman laid the foundation for modern bottom fauna investigation when he devised a closing dredge to bring up a known area of bottom. In the same year Petersen described a similar apparatus for marine work. With Ekman he shares the credit for introducing accurate sampling methods, without which bottom fauna investigation could have had only a limited development.

Following Ekman's paper of 1915, in which he published the first results obtained by the new method, we find a great increase in the number of investigators with a corresponding diversity in the viewpoint and application of results. Since the field has become too large to be adequately dealt with in a brief sketch we may mention only the more important tendencies and a few of the workers responsible for the present status of the study.

Gunnar Alm (1922) made the first definite attempt to correlate the amount of bottom fauna in a lake with its fish production, a departure from Ekman's work which had been rather distributional and ecological. In recent years European workers have studied large numbers of lakes and have made considerable progress in the study of lake types. Their division of lakes is based both on the predominant species in the bottom fauna and on the kind of bottom deposit found therein. Alm in Sweden, Oldstadt in Norway, Jarnefelt in Finland, and Lundbeck and Thienemann in Germany have contributed to this field, so that some one hundred lakes have been examined from the point of view of lake types.

In North America bottom fauna studies have been less extensive, involving about ten lakes. Birge, in 1922, improved the closing apparatus of the Ekman dredge, which was used, in its modified form, by his associates Juday and Muttkowski, in their work on Lake Mendota. Muttkowski (1918) began with a study of the shallow water with special reference to the insects. Juday (1922) completed it by investigating the fauna of the deeper water. In 1924, Juday published an account of the fauna of Green lake, a small deep lake in Wis-

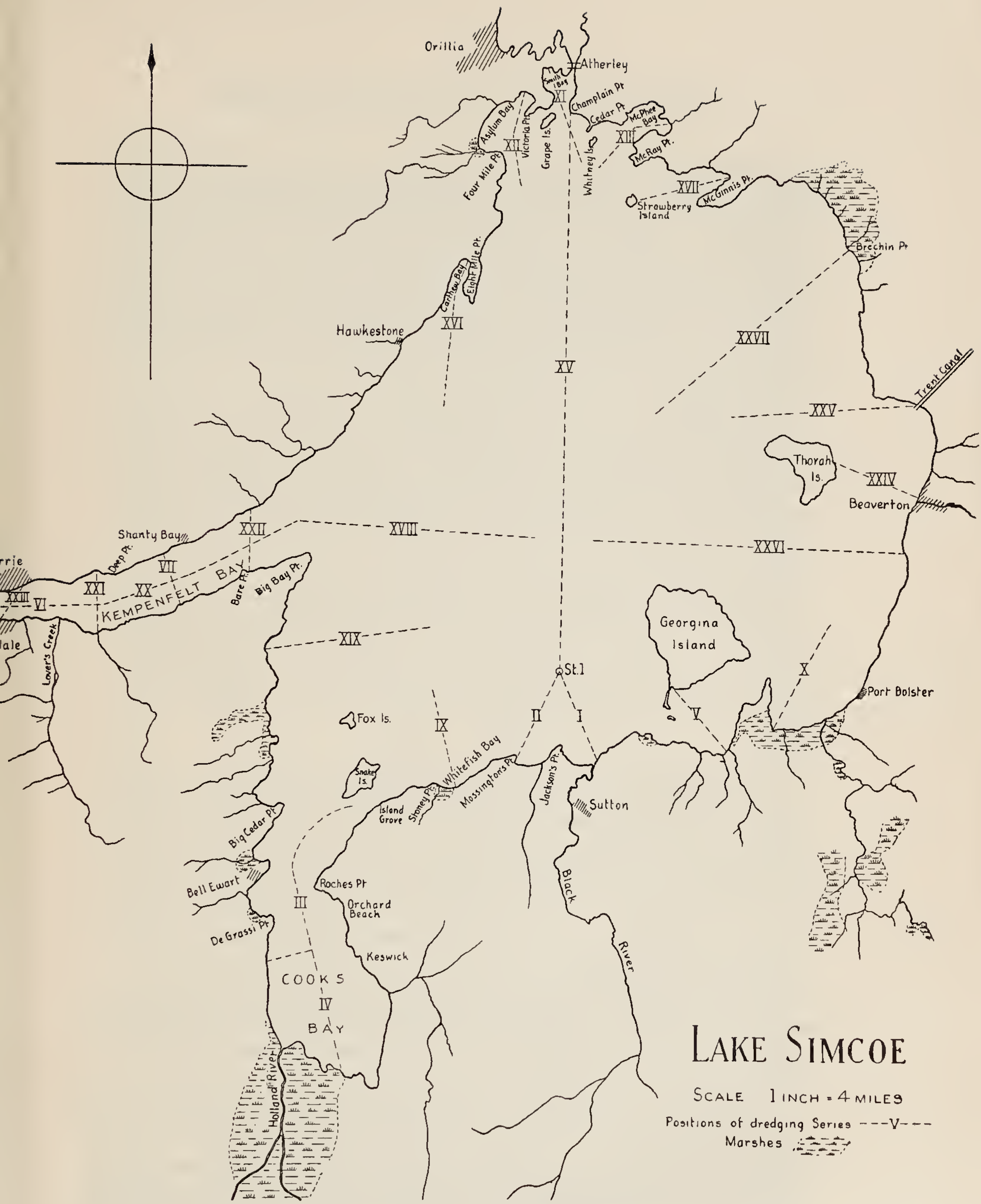
consin. Richardson made a noteworthy contribution in his study of the bottom fauna of the Illinois river and connecting lakes and in the subsequent records of changes in this fauna due to increasing sewage pollution. A survey of the bottom fauna of Oneida lake, in which the molluscs and their relation to fish were treated very thoroughly, was published by Baker in 1918.

In Canada the work has been limited to an investigation of Lake Nipigon carried on by Adamstone, 1922-24, in conjunction with the biological survey of the lake made by the Ontario Fisheries Research Laboratory. This work is of particular interest in being an account of a very large, deep lake quite unlike any other in which the bottom fauna has yet been thoroughly investigated. Lake Simcoe, while small in comparison with Nipigon, is relatively large as compared with the other American lakes mentioned above. Its intermediate nature makes it a valuable link in the correlation of conditions in large and small lakes.

GEOLOGY AND PHYSIOGRAPHY OF LAKE SIMCOE

Lake Simcoe, Lat. 44°N., Long. 79°W., is the fourth largest of the inland lakes of Ontario, having an area of 280 square miles. Situated 40 miles due north of Toronto it forms a link in that part of the Trent Valley system of waterways which empties into Georgian bay by way of Lake Couchiching and the Severn river. From Lake Simcoe's elevation of 720 feet (above sea level) the water falls to 581 feet at Georgian bay.

The depression in which Lake Simcoe is situated is part of the valley of the ancient Laurentian river (Coleman, 1922). In interglacial time this river drained the Lake Huron-Georgian bay region, running south from the present Georgian bay through the Holland river valley to Scarborough just east of Toronto. Glaciers blocked this valley by piling up an interlobate moraine which forms the present height of land midway between Toronto and Lake Simcoe. In post-glacial time this valley filled with water to form a bay of the great


Lake Simcoe
Scale 1 inch = 4 miles
Positions of dredging Series ---V---
Marshes
Orillia
Atherley
Smith Bay
Champlain Pt
Cedar Pt
McPhee Bay
McRay Pt.
Asylum Bay
Victoria Pt
Grape Is.
Whitney Is.
Four Mile Pt.
Strawberry Island
McGinnis Pt.
Brechin Pt
Carthew Bay
Eight Mile Pt.
Hawkestone
Trent Canal
Thorah Is.
Beaverton
Shanty Bay
Deep Pt.
Kempenfelt Bay
Bare Pt.
Big Bay Pt.
Lover's Creek
Georgina Island
St. 1
Port Bolster
Fox Is.
Whitefish Bay
Mossington's Pt.
Jackson's Pt.
Sutton
Snake Is.
Island Grove
Stoney Pt.
Big Cedar Pt.
Bell Ewart
Roches Pt
Orchard Beach
De Grassi Pt
Keswick
Black River
Cooks Bay
Holland River

Map 1.

Lake Algonquin which covered the area now occupied by Lakes Superior, Michigan and Huron and extended beyond their limits. Finally, deformation as described by Johnston (1916) lifted the land at the mouth of this bay, tipping the strata to leave a basin, Lake Simcoe, cut off from Lake Algonquin. Lake Simcoe, having originated in this manner, was probably of much greater area than at present and its flood waters cut their outlet to the northwest, forming the Severn river.

Geologically, the lake lies almost wholly in the Trenton formation with its extreme north end and Lake Couchiching extending through the Black river formation into the Precambrian area. The Trenton limestone is a thin, hard layer underlying the lake and completely covered by clays of glacial origin.

The present lake is somewhat rectangular in outline with two long finger-like bays, one on the west and one on the southwest. With the exception of these bays its shores are much exposed, a condition readily seen from the map and indicated by the shortness of its shore line in relation to its area.

The shore line, as measured from the Department of Railways and Canals chart, has a length of 123 miles, which is short for a lake 280 square miles in area. By calculation the shore development* is 2.27. If we add the shore line of the islands, for that, too, is essentially lake shore, we find a total of 144 miles. Detailed notes were made in the field as to the type of all this shore line and calculations based on these data indicate that of the 144 miles, 54 per cent. was stony, 33 per cent. sand and 13 per cent. supported vegetaton. These shore types will be discussed more fully in a later chapter with reference to the quantity and quality of their fauna.

The large proportion of exposed shore line magnifies the importance of wave and ice action both on the physical nature of the shore and on the life which it supports. Storms sweep

*The ratio of the shore line to the perimeter of a circle of the same area as the lake.

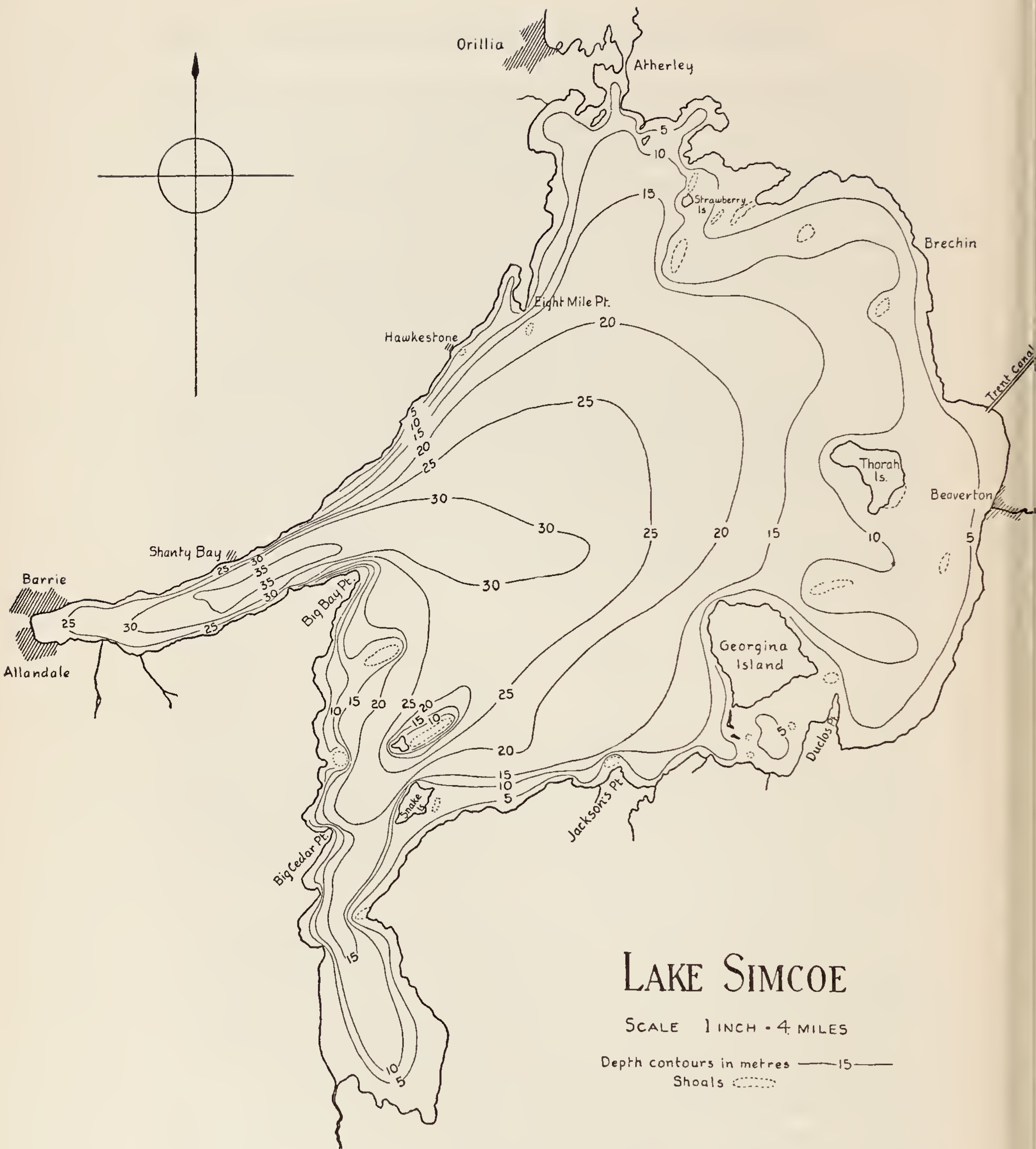
the lake and, crossing its diameter of roughly 15 miles, develop a wave action of considerable intensity. Although the eastern and southern shores are subjected to the most intense wave action, the remainder is also much exposed. In the spring great ice sheets through the action of the wind disturb the shore materials and denude it of vegetation. Champlain point and Grape island in the north end of the lake are excellent examples of the results of such action: their high steep banks are composed of loose boulders pushed up by the ice.

The average depth of Lake Simcoe has been determined as 17 metres (56 feet) and the maximum depth 44 metres(145 feet). Using the depths obtained in making 200 dredgings and 80 additional soundings, map number 2 has been constructed to show the distribution of depth in the lake. Contour lines have been drawn at intervals of 5 metres in depth from the shore down to a depth of 35 metres. Of the total area, 280 square miles, the separate depth zones make up the following proportions:

0- 5 metres	14%	20-25 metres	15%
5-10 "	15%	25-30 "	17%
10-15 "	16%	30-35 "	5%
15-20 "	17%	35-40 "	1%

From these figures it is seen that the depth zones from 0-30 metres are fairly similar in area and that a relatively small area of the lake (6 per cent.) has a depth of more than 30 metres. These data were the basis for the calculation of average depth as 17 metres.

The depth contours on map number 2 indicate that the deep water is in the central and western portions of the lake, Kempenfelt bay being particularly deep. In this portion of the lake the descent from shore into deep water is very rapid, in marked contrast with the gradual declination in the eastern part of the lake where large shallow areas are to be found. In the combined result the deep water of the western and central portions compensates for the predominance of shallow water in the remaining areas with the result that there is a uniform distribution of area with depth, *i.e.*, each


Orillia
Atherley
Strawberry Is
Brechin
Eight Mile Pt.
Hawkestone
Trent Canal
Thorah Is.
Beaverton
Shanty Bay
Barrie
Allandale
Big Bay Pt.
Georgina Island
Duclos Pt.
Snake Is.
Jackson's Pt.
Big Cedar Pt.
LAKE SIMCOE
SCALE 1 INCH - 4 MILES
Depth contours in metres ——15——
Shoals

MAP 2.

of the six depth zones from 0-30 metres contains about 16 per cent. of the total area of the lake. As might be expected, the shallower part of the lake contains many shoals and reefs, some of them as much as one mile in their longest dimension. They are predominantly rocky and often come very close to the surface of the water.

Rivers and streams emptying into Lake Simcoe drain a watershed of some 1,100 square miles, excluding the area of the lake itself. This area is largely cultivated land with a small amount of woods and some marsh. Three large streams empty into the lake along its southern margin, the longest of which is the Holland river with a length of 23 miles to its most distant source. In the lower eight miles of its course it flows through the large Holland river marsh and empties into Cook's bay. The Blackwater river is about 18 miles long and empties into the lake just east of Jackson's point. The Pefferlaw river (also locally known as Black river) is farther east, emptying into the bay just east of Duclos point. Some thirty other streams empty into the lake. A few are of considerable size, *e.g.* the Beaver river at Beaverton, but most of them are small in flow and less than 5 miles in length. The outlet through the Narrows at Atherley is a stream some 50 feet in width with a flow in the neighbourhood of 600 cubic feet per second at the normal low-water level.

THE PHYSICAL AND CHEMICAL CONDITIONS IN THE WATER

To illustrate the condition of the water in Lake Simcoe, table 1 has been constructed, showing five series of temperatures and water analyses taken at significant seasons.

These observations were all taken at station 1 (map number 1) in a depth of 21 metres of water. Other temperature series were taken at station II off Eight Mile point and in the deep water off Kempenfelt bay, but they add nothing to the information conveyed by the present series.

Observations on March 2, taken through an ice layer 18

TABLE 1. Selected observations of the physical and chemical conditions in Lake Simcoe taken during the years 1927-28 at station 1 (21 m.).

	March 2			May 19			June 20			July 15			Sept. 17		
	Temp. °C	O_2 p.p.m.	pH	Temp. °C	O_2 p.p.m.	pH	Temp. °C	O_2 p.p.m.	pH	Temp. °C	O_2 p.p.m.	pH	Temp. °C	O_2 p.p.m.	pH
Air........	−6.0			12.6			18.0			16.0			13.0		
Surface 0 m.	0.8	10.8	8.0	5.7	7.8	8.1	14.2	6.4	8.1	18.2	5.6	8.3	9.3	7.2	8.2
" 5 m.	0.77						13.1	6.5		17.9	5.5		9.3		
" 10 m.	0.78			5.6			12.8	6.1		16.9	5.2		9.2		
" 15 m.	0.79						11.25	5.6		11.3	4.9		9.3		
" 20 m.	0.79	9.45	8.0	5.2	7.4	8.0	11.05	4.3	8.0	10.3	2.9	8.1	9.2	6.8	8.1

inches in thickness, show a practically uniform temperature from surface to bottom and a plentiful supply of oxygen at all depths. It is evident that Lake Simcoe does not suffer from "winter stagnation."

The series taken on May 19 shows nothing unusual, but on June 20 the water was slightly stratified and the bottom oxygen down to 4.3 p.p.m. The maximum stratification observed was on July 15, when the bottom oxygen was as low as 2.9 p.p.m. At this time an attempt was made to determine the oxygen content near the mud. The apparatus in use was not altogether suitable for this experiment, and the lowest oxygen determination was found to be 2.0 p.p.m., the sample being taken from about 0.75 metres above the mud. The decrease from 2.9 to 2.0 p.p.m. in the lower two metres is suggestive of a considerable micro-stratification or "micro-schichtung" as Alsterberg (1922) has termed it (page 84). In at least one of the three seasons the stratification and lowered bottom oxygen was destroyed prior to August 30, when a bottom water sample from 25 metres contained 6.3 p.p.m. of oxygen.

The moderately high transparency of the water in Lake Simcoe is attested by the fact that Secchi's disc could be seen at a depth of 6 metres, the average of five determinations taken on the above-mentioned dates. The disc used was of white enamelled wood 9 inches in diameter. The hydrogen ion concentration of 8.1 indicates an alkalinity due in part to the limestone and marly clays of the vicinity.

In general the water may be described as clear, cool, well oxygenated and slightly alkaline.

APPARATUS AND METHODS

The experimental work consisted primarily of the collection and examination of the bottom fauna, including macroscopic and microscopic forms from various depths and types of bottom. To interpret the data resulting from this survey it was necessary to collect and examine the plankton, to make chemical analyses of the water and of the ooze,

plankton and bottom organisms and finally to study the food of the more important fishes.

The description of apparatus and methods is arranged in the following order:

I. Dredging and sorting
  (*a*) Limitations and sources of error in the technique.
  (*b*) Qualitative collection in deep water.
  (*c*) Records of dredging data.

II. Shore collecting.

III. Special apparatus for investigating the bottom deposits.

IV. Quantitative data and calculations.

V. Special methods of studying substances or organisms related to the bottom fauna.
  1. Fish food. 2. Plankton. 3. Bottom deposits. 4. Water analyses.

DREDGING AND SORTING

In this work the aim was to keep the technique as like that used in former work of the laboratory as possible in order to facilitate the comparison of results. Accordingly the methods were essentially those used by Adamstone (1924) on Lake Nipigon with such changes as were considered to be improvements. The Ekman dredge (Birge, 1922), plate I, figs. 1 and 2, with release was used to collect the material from an area of 500 sq. cm. or 77.5 sq. in. A strong portable windlass with a 3/16-inch steel cable was used to haul the dredge. The bottom sample was transferred from the dredge to wooden trays 18×10×4 inches lined with white oilcloth or in some cases to galvanized buckets. Depth was observed from a counter on the frame of the windlass and distance from shore was estimated for short distances or calculated from the speed of the boat for longer distances. Field records were kept of all observations and included notes on the character of the bottom, plants brought up, etc.

The samples were washed successively through three screens attached to wooden frames as indicated in diagram 1. The uppermost screen was of coppered wire mosquito netting with about 180 meshes to the inch. The lower screens were of silk bolting cloth, 480 meshes and 1,400 meshes to the inch respectively. These silk screens were a considerable improvement on the older cheesecloth and factory cotton variety both in allowing the mud to pass through more readily and in the ease with which they were cleaned. When the lower screen became clogged with fine clay it was found useful to float out the organisms by repeated additions of water after which they were picked up direct or by re-straining the supernatant liquid.

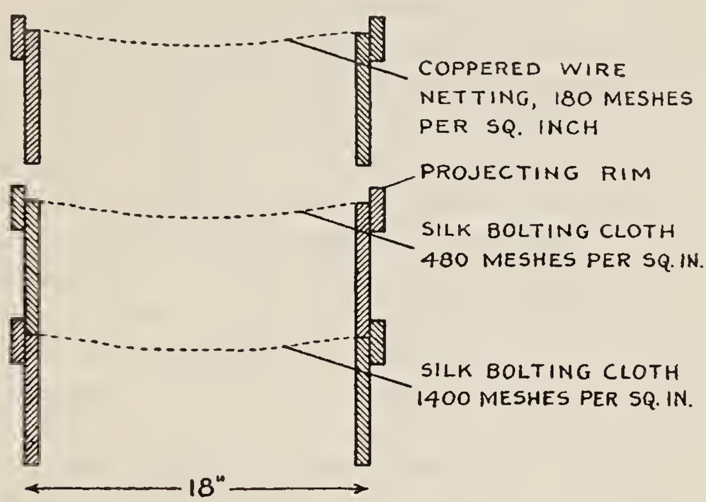


Diagram 1.—Showing a sectional view of the screening arrangement.

The organisms screened from the sample were usually taken direct from the screens and preserved in 70 per cent. alcohol. If the residue, *e.g.* pebbles or wood fragments, left on the screen was too great to allow this procedure, all of the material caught by the screens was returned to the tray with a little water. With the advantage of the white oilcloth background it was then possible to pick out the living organisms with ease.

Limitations and Sources of Error in the Technique

The dredge is not always successful in bringing up the whole 77.5 square inches of bottom and the fauna from this area. Incomplete sampling occurs in several kinds of bottom. Sand is frequently packed so hard that the jaws of the dredge only scrape the surface without penetrating deeply enough to collect all the fauna. Hard clay is even more difficult to sample, although it occurs only in restricted areas and is therefore relatively unimportant. Gravel or stone also prevent the closing of the dredge.

Hard bottom samplers have been devised (Knudsen, 1927) but the lightest model weighs more than 200 pounds and is therefore impossible to handle with the usual freshwater equipment. The heavy sampler described below under the investigation of bottom ooze was too small to be used in quantitative examination of the macrofauna. For stone bottom no satisfactory quantitative sampler has been devised. For qualitative work, J. L. Hart of the Ontario Fisheries Research Laboratory, has arranged a suction pump which is very effective. The apparatus consists of a simple force pump with large valves, to allow the passage of small stones, etc., a 20-foot length of 1 ¼-inch rubber hose and a 25-foot pole. The operator in the boat uses the pole to direct the lower end of the tube while an assistant manipulates the pump. A coarse screen on the intake prevents it from clogging and a fine screen hanging over the side of the boat strains the water from the pump and catches the bottom organisms.

Organisms are sometimes lost when the dredge has been brought to the surface, being carried out with the water that drains from its corners. When sampling bottom, which is covered with vegetation or coarse debris, the jaws are frequently prevented from closing completely. Small Crustacea such as the Entomostraca or Amphipoda may be lost in this manner. After the first fifty dredgings had been taken, this loss was prevented by placing a short-handled dip net under the dredge as it reached the surface. The net was 18

inches in diameter and made of silk bolting cloth with about 480 meshes per square inch.

In screening the sample, care will prevent the loss of material over the edge of the screen. Although the lower screen stops the passage of all macroscopic organisms it is difficult to pick minute organisms from a mass of debris. Small transparent nematodes would escape observation were it not for their great activity which attracts the attention of the searcher. Minute red chironomid larvae are picked out quite readily from a dull background. Some organisms have no such distinguishing characteristics, for example, it is almost impossible to separate minute Sphaeriidae from a residue of coarse yellowish sand.

Each of these limitations in the technique may result in some loss from the organisms which inhabit the unit area which we wish to sample. This effect, although unimportant from a qualitative point of view, causes a varying amount of inaccuracy in the quantitative estimates. The amount of the loss, being dependent upon two variable factors, the quality of the fauna and the kind of bottom deposit, is in itself quite variable and not easily corrected.

A further possibility of error arises from the uneven distribution of the fauna itself. The unit area, 500 square centimetres, brought up by the dredge, is as large as can be conveniently handled with a light windlass in a small boat. In some cases it is not large enough to bring a fair sample of certain organisms. A test of this variation was made on August 3, 1929, during the investigation of a lake in northern Saskatchewan. In a part of the lake which was 9 metres deep the bottom was a rich organic ooze and thickly populated with *Chironomus plumosus*. Eight dredgings were taken in a circle 40 feet in diameter. The number of *C. plumosus* per dredging averaged 25, but varied from 15 to 41. The maximum deviation in this case amounted to 64 per cent. of the average population. Such a result indicates the necessity of taking large numbers of samples to reduce the error resulting from uneven distribution.

Seasonal variation in the bottom fauna (page 114) con-

stitutes another difficulty which, though independent of the method of sampling, makes it necessary to distribute the dredging over all types of bottom and throughout as many seasons as possible in order to get a fair sample of the bottom population.

QUALITATIVE COLLECTIONS IN DEEP WATER

The suction pump has already been mentioned (page 18) as a method of making qualitative collections from the bottom. A second apparatus which was operable at greater depths was a dragnet with runners (plate II, figs. 4 and 5) resembling that described by Reighard (1919). The net had a triangular opening 8 inches to the side, and three runners of brass. When the net was in use additional weight was added in the form of two 12-inch pieces of 1/2-inch lead pipe, one of which was slipped over each of the two runners which were to come in contact with the bottom. The outer net of heavy cotton served to protect an inner net of silk bolting cloth, 180 meshes to the inch, equipped with a simple bucket that facilitated the removal of the haul. The net was particularly useful in collecting amphipods, insect larvae and the larger plankton Crustacea which live near the bottom.

RECORDS OF DREDGING DATA

The data obtained in dredging were recorded in tables, an example of which is given below. Each table contained the results of one series which was a convenient group, ten or less, of dredgings in a chosen habitat or area. In most cases a series was begun near the shore line and continued into the deep water, dredgings being taken at intervals small enough to indicate the changes in fauna as the series progressed. Over long distances it was often found convenient to begin a second series where the first finished in order to complete the study of a given area.

The distance from shore was recorded in yards or miles and depth was expressed in metres. While the use of two systems of measurement is somewhat confusing, circumstances made this practice unavoidable. Distances on the water could be measured more accurately in the familiar

units of yards and miles and these units are used in all the available maps and charts. For depth it was thought advisable to use metres in order to make our results comparable with those of a large number of other investigators who had used this unit. Certain signs were used to indicate the character of the bottom, as follow:

m—Mud: soft oozy material with varying quantities of organic detritus in its surface layers and usually on a substrate of soft grey clay.

s—Sand.

c—Clay: hard clay (not applied to the softer type of clay found in deep water).

g—Grit: coarse sand.

gr—Gravel: pebbles and stones not more than 3 inches in diameter.

r—Rock: stones or boulders.

ma—Marl: limy bottom consisting mostly of more or less finely broken mollusc shells with a mixture of clay.

These signs were combined to represent other types of bottom, *e.g.* s/c indicates sand on clay.

TABLE 2.—An example of the dredging records.

Dredging No.	1	2	3	4	5	6	7	8	Totals
Depth in metres	1.5	3.5	8	10	11.5	16	18.5	20	
Distance from shore	100 yds.	250 yds.	600 yds.	1 mi.	2½ mi.	4 mi.	5½ mi.	7 mi.	
Character of bottom	s	s/gr	s	g/c	s/m	m	m	gr/m	
Gastropoda	....	7	8	14	2	23	1	2	57
Sphaeriidae	....	6	5	5	....	11	1	2	30
Chironomidae	....	20	5	62	3	49	5	8	152
Ephemeridae	....	1	....	5	....	7	11	2	26
Trichoptera	....	3	....	....	....	....	....	1	4
Amphipoda	....	27	6	14	....	....	....	....	47
Oligochaeta	2	....	2	....	....	2	....	1	7
Totals	2	64	26	100	5	92	18	16	

Table 2. An example of the dredging records.
Series XXVII. June 16, 1928.
Begun 100 yards south of Brechin point and continued southwest for a distance of 7 miles.
Dredging 1. Clean hard sand with ripple marks.
2. Gravelly sand with some *Chara*.
4. Scattered growth of *Chara*.
8. Unusual bottom type—gravel scarce at this depth.

SHORE COLLECTING

In the shore zone (0-1 metres) special methods of collection were used. In locations where the bottom was soft and the fauna not too scanty the dredge was used as in the open water. If the bottom were stony, weedy or otherwise difficult to sample, a unit area was marked off by a square frame 18 inches to the side. This unit was large enough to give a convenient sample and its area was four times that of the Ekman dredge. The sample from such an area was dipped up with a heavy scoop and screened through the usual sieves. Stones were thoroughly washed and the water poured through the screen to catch any clinging organisms. For qualitative collections a heavy metal dipper, capacity of 1 quart, with its bottom replaced by one of copper netting, was found very useful. A dip net and a small seine were used for the same purpose.

SPECIAL APPARATUS FOR INVESTIGATING THE BOTTOM DEPOSITS

In studying the composition, layering and microfauna of the bottom deposits in deep water, the dredge is not altogether satisfactory. It is inconvenient to lift the lids and examine the contents of the dredge from the top, and the layering is greatly disturbed when the contents are turned out. Moreover, the water which drains from the top of the sample disturbs and carries off part of the surface detritus.

In order to bring up a portion of the bottom intact, with the surface ooze and the water still in place above it, a heavy sampler was devised as follows:

THE HEAVY BOTTOM SAMPLER

The action of this sampler depends on its weight which causes a 4-inch brass pipe to sink into the bottom to a depth of several inches. This pipe is lined with a removable cardboard sheath paraffined to make it waterproof. When the tube has penetrated the bottom a brass messenger let down the cable, releases a rubber plug which closes the top end of the tube. When the apparatus has been hauled to the surface, a cork is inserted in the lower end of the sheath and the latter removed with its sample. A second cork is placed in the top of the sheath and the whole taken to the laboratory.

Details of the construction of this sampler may be seen in plate I, figs. 3, 4 and 5.

A is the brass tube 4 inches inside diameter, 1/2 inch in thickness and 11 inches long. It is slightly sharpened at the lower edge to aid in penetrating the bottom and has a flange on the upper inside surface to prevent the cardboard sheath slipping upward.

B is the broad flange which prevents the sampler from sinking too deeply into the bottom. A much heavier flange was provided for hard bottom but was seldom found necessary.

C is the release which when struck by the messenger releases the plunger.

D is the rubber plug on the lower end of the plunger. This plug fits exactly into the bevelled upper end of the tube *A*. The plunger is forced down by

E the spring which is compressed when the apparatus is "set."

Fig. 5 is the paraffined cardboard cylinder used within the tube *A*.

The sampler measures 30 inches in height and weighs 35 pounds.

When the sample had been taken to the laboratory the water was siphoned from the upper part and strained through a net of plankton silk. The upper layer of detritus was taken off with a pipette for microscopic examination. The cardboard cylinder was then cut down with a sharp knife to allow a microscopic and chemical examination of the mud layers which were practically unmixed by the sampling process.

This sampler was used chiefly in the deep water. In shallow water the type of bottom was ascertained before the sampler was lowered to avoid damaging the lower end of the tube on stones. As might be expected, loose sand would fall out of the tube before it reached the surface. In fine, well-packed sand the sample was usually retained until the operator was able to reach down and insert the lower cork.

For the qualitative examination of the microfauna inhabiting the upper ooze layer a more convenient sampler was devised which was called the ooze sucker. This instrument was an adaptation of the idea used by Richardson (1921) in his apparatus for collecting bottom ooze in the Illinois river. Richardson's original apparatus was limited to depths of not more than 15 feet since it was operated with a wooden handle.

The essential parts of this sucker were a rubber bulb of 50 c.c. volume, which was attached to an obtuse funnel of sheet copper. A frame, which served to keep the funnel upright when it touched the bottom, bore two arms which could be made to compress the bulb but might be released by sending a messenger down the cable. The mouth of the funnel (3 1/2 inches diameter) was covered with a coarse metal screen, 150 meshes to the inch, which prevented the obstruction of the tube by coarse debris. Six small holes (1/16 inch in diamter) were bored through the funnel 1/2 inch from its circumference. When the edge of the funnel was resting on the bottom mud these openings allowed the water to enter, wash across the surface of the mud and be drawn up into the bulb. When hauled to the surface the bulb was removed and its contents forced into a 2-ounce bottle for microscopic study in the laboratory. In plate II the ooze sucker is shown before (fig. 1) and after (fig. 2) its release.

This instrument was easily and successfully used in a variety of depths and on most kinds of bottom.

The deeper bottom deposits were sampled by lowering an 8-foot length of 1 ¼-inch galvanized pipe through a hole in the ice. The weight of this pipe was 14 pounds and it could be made to penetrate as deeply as 6 feet into the mud of the deep water deposits. A small quantity of the mud brought up in the lower open end of the tube was removed for examination. The depth to which the tube had penetrated was measured by letting a sounding iron down to the surface of the ooze and pulling both ropes up together. The distance between the sounding iron and the lower end of the tube was then equal to the depth of penetration.

QUANTITATIVE DATA AND CALCULATIONS

In the numerical study of the bottom population per unit area the dredging results were directly applicable and accurate within limits as suggested on page 18. In determining the quantity of organisms per unit area, dry weight was used as a unit rather than live weight. The live-weight method is less convenient from several points of view. It increases the complexity of the field work and a uniform standard of "dryness" in living specimens is very difficult to maintain. It is probable that dry weight is more indicative of the food value of bottom organisms than is the live weight, since the water content is not nutritive matter. The total organic nitrogen is a better index of nutritive value than either live or dry weight, but less easy of application.

The average dry weight of individual bottom organisms was determined by drying large numbers of each species to a constant weight. For this purpose the specimens were placed in crucibles in an electric oven and submitted to a temperature of 50°C. over a period of 24 hours. In some cases, *i.e.* chironomid larvae and ephemerid nymphs, the specimens varied so greatly in size that it was found advisable to divide them into groups of large, medium and small, the average weight of each group being determined separately.

The advantages of this method are that it leaves the most of the specimens for further qualitative or systematic work, and that it consumes much less time than the actual drying and weighing of the organisms from each individual dredging.

As a check on the accuracy of this procedure the organisms from 15 dredgings were classified and the weight calculated. The organisms were then dried and weighed and the actual weights compared with the calculated figures. In no case was the discrepancy greater than 25 per cent. with the average deviation being 9.5 per cent. It is therefore probable that the error is of no greater magnitude than that introduced by the uneven distribution of organisms as discussed on page 19. In cases where particular importance was attached to the amount of organisms taken in a dredging the actual dry weight was determined by the method described above.

Mollusc shells have always been a stumbling block in recording the amount of bottom fauna. Certain workers have included the total mollusc weight in the final figure, which we think is not advisable since mollusc shells are not a nutritive part of the bottom fauna. If this is done the resultant estimate is distorted, especially in cases where molluscs form a large part of the fauna. Others have stated production, both including and excluding the molluscs, which is better but not perfect, since neither figure is comparable to that from another location with a different proportion of mollusca in the fauna. We have adopted what we believe to be the best method in determining the shell content of different types of molluscs and deducting the shell weight from the total dry weight. The resultant dry "body weight" should be fairly representative of the nutritive value of the mollusc in question.

SPECIAL METHODS OF STUDYING SUBSTANCES OR ORGANISMS RELATED TO THE BOTTOM FAUNA

FISH FOOD

The food of fishes in the lake was determined by the examination of stomach contents, special attention being

given to the food of bottom-feeding fish. The fish were taken at different seasons and by a variety of methods, the most important being the use of gill nets of meshes ranging from 1 1/2 to 5 inches. Other specimens for stomach analysis were taken in seines and by angling and spearing. The contents of stomach and intestine were preserved in a solution of formalin, and later submitted to macro- and microscopic examinations in the laboratory.

PLANKTON

In studying the general relations of bottom fauna to plankton the net plankton only was considered. Two nets were used, one with a large mouth to take samples of sufficient quantity for chemical analysis, the other a standard closing net. The former net was of no. 20 silk bolting cloth, with a circular mouth 18 inches in diameter. The shape was that of a simple cone with a height of 3 feet. The lower end of this net was provided with a bucket similar to that used in the "Wisconsin" net as described below.

The closing net used was of the type described by Juday (1916). The mouth, with an inner diameter of 12 cm., is at the top of a truncated cone of heavy cotton. The lower straining cone was of no. 20 silk bolting cloth and was equipped with a standard removable bucket at its lower end. The net was closed at any depth by allowing a messenger (a brass weight) to slide down the line and trip the closing device. In proportion to the area of this mouth, this net was much more efficient than the larger net, due, of course, to the upper truncated cone which reduces the overflow as the net is hauled up. The Juday closing net had, at the end of the first season, an efficiency of about 63 per cent., determined in the following manner. A column of water of known volume was strained through plankton silk identical with that of the net to be tested and the catch of organisms was counted. The net was then drawn through an exactly similar column of water and its catch compared with the former. The effi-

ciency of the net was shown by the fact that it collected 63 per cent. of the plankton which, as the former experiment had shown, might have been collected from this given column of water. The coefficient of efficiency was thus determined as 1.6.

The larger net, with mouth 18 inches in diameter, was calibrated by drawing it through the same column of water as the closing net of known efficiency, and subsequently comparing the catch. By this method the efficiency of the larger net was calculated as 37 per cent. of the Juday net, and its factor accordingly was 4.32.

The efficiency of a net varies with its age since the meshes tend to become clogged and lessen the straining capacity. The large net, 18 inches in diameter, was kept for a specific purpose, making total vertical hauls in the vicinity of certain dredgings, so that the total number of hauls did not exceed fifty. It is thought that these fifty hauls did not appreciably clog the meshes, so the efficiency factor 4.32, determined when the work was completed, does not differ greatly from the average efficiency during the use of the net. It is obvious that the efficiency of a net varies with the kind and abundance of plankton and with the age of the net even if the method of using such a net is uniform. In spite of these difficulties it is considered better to apply any possible correction to the data in order to make it comparable to that obtained in other locations and by other workers.

The greater number of plankton collections were total vertical hauls with the large net. These were supplemented by vertical series and surface tows taken by the closing net. The near-bottom plankton was also collected by means of the triangular runner net described on page 20.

Analyses of the plankton hauls were microscopic, volumetric, dry weight and chemical, according to the purpose for which the sample was taken. The volume of a plankton catch was measured by allowing it to settle in a graduated glass cylinder (inside diameter of 1 cm.) over a period of 24 hours. Dry weight determinations were made with the technique described on page 25 for bottom organisms. The

only chemical analysis of the plankton was a determination of the total organic nitrogen content of the plankton. Difficulties encountered in the use of the usual microchemical technique for determination of total organic nitrogen resulted in the adoption of the following method, which is a modification of the macro Kjeldahl procedure. The latter was not applicable in its usual form due to the small quantity of nitrogen (0.5 to 3.0 mgm.) in the sample.

The plankton sample was placed in a 100 cc. Kjeldahl flask with a 1 cc. conc. sulphuric acid and the liquid evaporated to about 10 cc. Two cc. additional acid were then added along with 1 gm. potassium sulphate, a few drops of 5 per cent. solution of copper sulphate and a glass bead. Digestion was accomplished by heating over a micro burner until the solution turned green, the top of the flask being covered with a watch glass when dense white fumes began to appear. When the solution had cooled, 7 cc. water were added for every one cc. of acid used. The method so far is similar to that used in any microchemical nitrogen analysis such as that of urine. Nesslerization was, however, impossible because of the large proportion of acid added in the digestion process. A distillation process was therefore used with an apparatus similar to that used by Bock and Benedict with the substitution of the 100 cc. Kjeldahl flask for the pyrex tube used by these workers. After adding pumice to prevent bumping, the apparatus was connected and 30 cc. of a 50 per cent. solution of sodium hydroxide added for each cc. of acid used in digestion. The ammonia was distilled off into N/70 hydrochloric acid. The condenser was disconnected and washed down with a small amount of distilled water. To insure the complete liberation of ammonia another 3 cc. of sodium hydroxide was added, the condenser coupled and the mixture boiled for two minutes more. The titration was then made with N/70 sodium hydroxide, a mixture of methyl red and methylene blue serving as indicator. In the final titration, 1 cc. of N/70 NaOH solution is the equivalent of 0.2 mgm. of nitrogen.

Bottom Deposits

Samples of the bottom deposits, especially the soft ooze of the deeper waters, were examined both physically and chemically. The former examination entailed a microscopic study of the constituents of various layers in the bottom deposits. The chemical analyses of the deposits were designed to show the comparative amounts of organic material in different areas and the vertical distribution of this material through the bottom layers. Analyses included the determination of free ammonia, albuminoid ammonia, nitrates, nitrites, and total organic nitrogen. They were carried out under the supervision of A. V. De Laporte and with the technique described by him (1920). Samples of the sediments from the deep water have been examined by E. M. Kindle, who is interested in the mineral and microscopic nature of bottom deposits from the point of view of stratigraphical geology.

Water Analyses

The standard methods used in fisheries investigation were adhered to in the chemical and physical examination of the water. Temperature was determined with a deep-sea reversing thermometer (Negretti and Zambra). The transparency of the water was tested with Secchi's disc, a wooden disc 9 inches in diameter and covered with white enamel. Determinations of the dissolved oxygen were made by Miller's method (De Laporte, 1920) and the hydrogen ion concentration by means of the La Motte colorometric equipment.

Part I

The Survey of the Bottom Fauna

A. THE QUALITATIVE EXAMINATION OF THE FAUNA

The bottom organisms which are the subject of the study include all the macroscopic bottom living forms from the shore line to the deepest part of the lake. The shore fauna

is so rich and varied that it cannot be dealt with thoroughly in a general survey. For this reason the work on the shore area was confined to a quantitative analysis of the fauna with a determination of its typical and abundant forms. In the open water a more intensive qualitative examination was possible, and the resulting information more useful since the open-water fauna is more intimately associated with the fisheries problems of the lake than is the shore fauna.

Preliminary observations have been made on the micro-fauna which inhabits the bottom ooze of deep water. Since this is a new field, much of the time was occupied with the development of adequate sampling methods. A description of the apparatus used is given on page 23.

In referring to the occurrence and distribution of living organisms we make constant use of the term "depth zone." In this study we have made an arbitrary division of the bottom into 5 metre ranges, breaking the lake's depth of 45 metres into 9 zones. In addition to this we recognize in Lake Simcoe three larger divisions, marked out by differences of a biological, physical and chemical nature. Similar zones have been recognized by other limnological investigators who have frequently seen fit to make secondary divisions of these major zones. The exact limits of the zones as described by different workers seldom agree, due no doubt both to ecological differences in the bodies of water under investigation and to differences in interpretation. To prevent any misinterpretation of the terms as used in the present paper we include a definition of the three major zones and their distinguishing features.

The Littoral Zone. 0-5 metres. This zone is marked by variable conditions of temperature, the greatest water movement, abundant oxygen and the greatest light supply. The bottom may be of sand, stone or mud and frequently supports rooted aquatic plants.

Sublittoral Zone. 5-14 metres. The sublittoral zone is intermediate in position and character between the other two zones. The water is subject to moderate movement and variation in temperature. The light penetration is poor and

the larger rooted aquatic plants absent. Sand and stone bottom are less frequent than in the littoral.

Profundal Zone. 14-45 metres. The profundal zone is an area of typical deep water conditions with relatively little water movement, a low uniform temperature, oxygen at times scarce, light penetration at a minimum and the bottom deposits usually soft and muddy.

The main groups represented in the macrofauna, or larger bottom population of the lake, are the Oligochaeta, Crustacea, Insecta and Mollusca. The remaining part of the fauna, which is much smaller in quantity and in general less important, includes representatives of such groups as the Porifera, Coelenterata, Bryozoa, Turbellaria, Nematoda, Hirudinea and Hydracarina. Some of the smaller groups have received little attention, since the primary object of the survey was not a systematic study but rather a consideration of the bottom fauna as a whole and its relation to life of the lake.

MACROFAUNA—ANNOTATED LIST OF ORGANISMS WITH NOTES ON DISTRIBUTION, NUMBERS AND ECOLOGY

PORIFERA

Spongilla sp. A small sponge of this genus was found encrusting stones near the outlet of the lake at Atherley. A similar if not identical form was found on the rocky shore of Snake island.

COELENTERATA

Hydra fusca L. Submerged plants were the most frequent habitat for this species. While most commonly attached to *Nymphaea* or the potamogetons, scattered individuals were taken in dredgings within 100 metres of shore and at depths of 3 metres or less.

BRYOZOA

Plumatella sp. This bryozoan was collected from submerged logs in the north end of Smith's bay. It forms a

scattered covering on the rotting wood just below the water level.

Cristatella sp. Statoblasts of this form were taken from the bottom ooze in shallow water as well as in plankton and fish stomachs.

TURBELLARIA

Planaria sp. A species of *Planaria*, probably *P. maculata* Leidy, was collected in various parts of the lake. Most of the specimens were found at depths of from 1 to 6 metres among beds of *Chara* and on solid clay or marl bottom.

NEMATODA

The nematodes taken during the survey have been examined by Dr. G. Steiner of the U.S. Dept. of Agriculture. He finds three species.

Hydromermis acrostoma n. sp.
Hydromermis rawsoni n. sp.
Hydromermis sp. (not yet certain).

Dr. Steiner expects to publish descriptions of these species in the near future.

OLIGOCHAETA

The oligochaete fauna of the deep water all belonged to the family Tubificidae. In shallow water were found a lumbriculid and a semi-aquatic species of *Helodrilus*, neither of which was abundant.

Limnodrilus. Members of this genus were most abundant in the 0-5 metre zone with a gradual decline in numbers down to 20 metres and scattered individuals as deep as 30 metres.

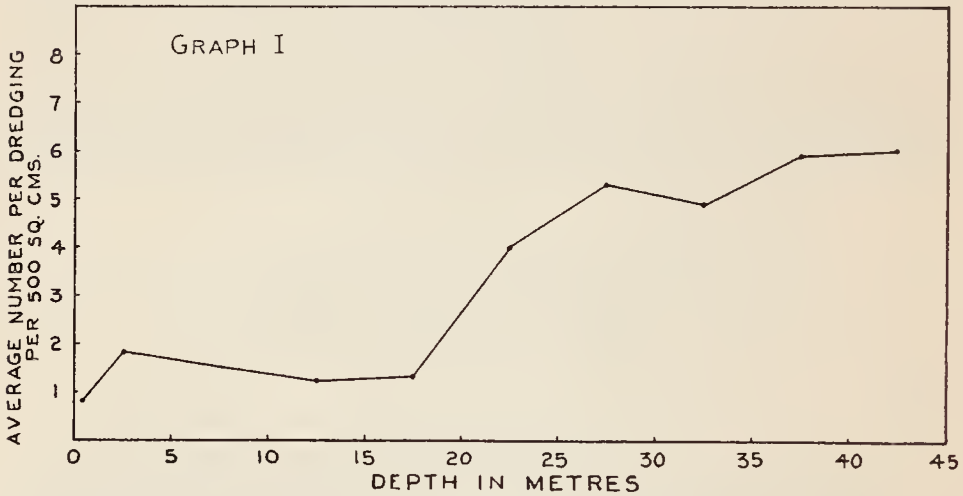
Tubifex. There were at least two species of *Tubifex* present. One, a slender form with long setae, was confined to the littoral zone. The other group, which was more abundant, was found first in 15 metres of water, increasing to a maximum between 30 and 35 metres and continuing in large

numbers to the deepest parts. The *Tubifex* group was found almost exclusively in mud bottom, while *Limnodrilus* was taken in a variety of habitats including sand, mud or *Chara* beds.

Lumbriculus sp. A large *Lumbriculus* was found in moderate numbers from shore down to depths of 3 metres. Most of the specimens were taken close to shore.

Helodrilus sp. A semi-aquatic member of this genus was collected at depths of 0.2 to 0.6 metres in sheltered bays, usually from a peaty bottom.

The distribution of Oligochaeta with reference to depth is shown in graph 1. The number of individuals decreases



GRAPH I. The distribution of Oligochaeta according to depth.

slowly from shore to a depth of 12 metres. Such a minimum in the sublittoral is a frequent occurrence in the distribution of bottom organisms and will be discussed in connection with the distribution of chironomid larvae (page 54). Proceeding from 15 metres into the profundal zone we find a rapid increase from 17 to 25 metres with a maximum abundance which is maintained into the deepest water. The number of oligochaetes in the profundal zone is almost four times that of the combined littoral and sublittoral zones. In this deeper area are found chiefly *Tubifex*, while *Limnodrilus* is largely confined to the upper 20 metres.

The distribution of Oligochaeta in Lake Simcoe is much more uniform than that in Lake Nipigon. In the latter lake the maximum number was found at a depth of 100 metres, while two minor maxima occurred at depths of 10 and 50 metres.

Although the oligochaetes make up a comparatively small part of the profundal fauna, they play an important rôle in the transformation and circulation of food materials. This function will be dealt with in Part II.

HIRUDINEA

The leeches collected during the course of the investigation have been identified by Professor J. P. Moore of the University of Pennsylvania. He reports 10 species which are listed in the following account:

Glossiphonia nepheloidea (Graf.). A single specimen of this species was brought up from hard sand at a depth of 5 metres.

Helobdella stagnalis (Linn.). This is one of the most abundant leeches in the lake and it exhibits a very general distribution. On mud bottom it is most frequent at depths of 0 to 2 metres, but is found as deep as 18 metres. It ranges alike over clay, sand or stone and on exposed points or in weedy protected bays.

Placobdella rugosa (Verr.). Small numbers of this species were collected from the rocky shores of Fox island.

Actinobdella triannulata Moore. This species was described by Moore from Lake Nipigon in 1924. In Lake Simcoe it was taken from sandy *Chara* bottom at a depth of 2 metres.

Piscicola punctata (Verr.). This fish leech was collected in numbers from whitefish and perch and from gill nets set in shallow water. A few specimens were taken on a gravel bar at the Sand islands.

Haemopis marmoratis (Say). This leech was collected in several parts of the lake from stony shores. A single specimen was found on the muddy shore of Smith's bay in the

act of devouring a large dragonfly nymph (*Hagenius brevistylis*).

Haemopis grandis (Verr.). This is the largest leech of the lake. It was taken most frequently from exposed rocky shores such as that of Fox island. Three large specimens were brought up with gill nets set at depths of 3 to 5 metres.

Erpobdella sp. Immature specimens of this genus were collected in large numbers from the shores of Snake island.

Nephelopsis obscura Verr. *Nephelopsis* was widely distributed about the lake, being found on almost every stony shore.

Dina parva Moore. This small leech is probably the most abundant in the lake, though more limited in habitat than *H. stagnalis*. It is confined to stone or clean sand bottom, being especially abundant on the former. Stomachs of perch and bass were found on several occasions to contain one or two specimens of this leech.

Being relatively small in numbers and practically confined to the shore area, the leeches are not an important link in the life of the lake. Their activity as parasites and slight value as fish food are probably no more important than their less noticed work as scavengers.

CRUSTACEA

The Crustacea of Lake Simcoe are well represented in the littoral areas but sparse in the deeper water. The larger forms are successfully collected with the dredge but Entomostraca were often washed out with the water which drained from the dredge after it left the water. After the introduction of a dip net (page 18) to strain this overflow, a considerable increase was noted in the number of Entomostraca collected.

Cladocera

Seven species of Cladocera were taken in the bottom samples.

Sida crystallina (Müller).
Daphnia longispina var. *hyalina* (Leydig).

Illyocryptus sp.
Acroperus harpae Baird.
Alona sp.
Eurycercus lamellatus (Müller).
Camptocercus rectirostris Schroedler.
Chydorus sphaericus (Müller).

Of the above forms *Illyocryptus*, *Acroperus* and *Eurycercus* are found very close to or right in the uppermost layer of the ooze. *Eurycercus* was the most abundant of these bottom-living forms. *Alona* and *Camptocercus* are usually within 0.5 metres of the bottom, while the occurrence of *Sida*, *Daphnia* and *Chydorus* is less significant for they are distributed throughout all depths of the water.

Copepoda

The following copepods were taken with the dredge:
Diaptomus minutis Lilljeborg.
Epischura lacustris Forbes.
Cyclops sp.
Canthocamptus sp.

None of these forms can be regarded as exclusively bottom types although *Canthocamptus* is found more frequently near the bottom than in the upper water.

Ostracoda

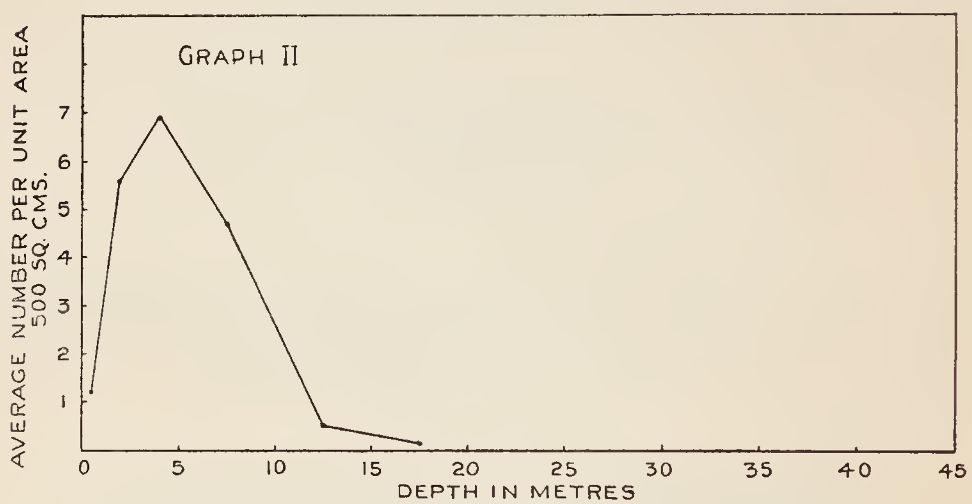
Candona spp.
Limnocythere sp.

No specific determinations have been made in this group but there were at least two species of *Candona* and possibly two of *Limnocythere*. Ostracods are abundant from shore to a depth of 10 metres. From this depth to 30 metres we find a small but regular occurrence and a slight increase from 30 to 45 metres. These deeper water forms are all of the genus *Candona*.

Of the Entomostraca mentioned above, we may regard *Illyocryptus*, *Acroperus*, *Eurycercus*, *Canthocamptus* and the ostracods as bottom forms. The remaining forms are to be considered as chiefly limnetic with an occasional occurrence on the bottom.

Mysidaceae

Mysis relicta Loven. The scarcity of *Mysis* in the lake is one of the outstanding features of the bottom fauna. Only five specimens were taken during the three years of the investigation. Four of these were from fish stomachs (ling and whitefish) and one was brought up by the dredge from a depth of 32 metres. Continued attempts were made to find more of this species, chiefly by towing in the deep water, but always without success. Coupled with the absence of any deep water Amphipoda (see below) the scarcity of *Mysis* constitutes a noticeable lack in the bottom fauna as fish food.



Graph II. The distribution of Amphipoda according to depth.

Amphipoda

Gammarus limnaeus Smith.

Hyalella knickerbockeri Bate.

The two species of Amphipoda taken were of very limited distribution. *G. limnaeus* was found only in the shore zone 0 to 1 metres and was not numerous. *H. knickerbockeri* was confined to the littoral and sublittoral zones with its maximum abundance in the former at a depth of 4 metres. The abundance of *H. knickerbockeri* in the shallow water, especially on beds of *Chara*, constitutes an important source of fish food.

The absence of Amphipoda from the deeper water of Lake Simcoe is difficult to understand. The geological history of Lake Simcoe (page 8) indicates that it was connected with Lake Algonquin in post-glacial times. Lake Huron, which represents one remnant of Lake Algonquin, has both *Pontoporeia* and *Mysis* in its fauna. It is therefore probable that these forms were once present in Lake Simcoe. That *Pontoporeia* has disappeared and *Mysis* is almost gone may be due to the warming up and decrease in depth of the lake subsequent to its formation. Lundbeck (1926) speaks of relict Crustacea as the only "kaltstenothermic" species in fresh water lakes, thereby indicating their preference for cold water. Most deep lakes, for example, Lake Nipigon and Lake Ontario, have a copious supply of *Mysis* and *Pontoporeia* in their lower strata where it is utilized by whitefish and ciscoes.

DECAPODA

Cambarus virilis Hagen.
Cambarus propinquus Girard.

C. virilis was taken from all kinds of hard bottom and at depths ranging from shore down to 6 metres. Large specimens were frequently brought up with gill nets, set in 4 to 5 metres of water. *C. propinquus* was never taken at depths greater than 1 metre. A further contrast was noted in that immature specimens of *C. propinquus* were frequently found on gravel or stony shores while the specimens of *C. virilis* were, with one exception, adults. Both species were found in bass and perch stomachs, but *C. virilis* was more common than *C. propinquus*.

ISOPODA

Mancasellus tenax. This species was collected from depths of 1 to 16 metres and in various parts of the lake. In the littoral or sublittoral zones it was always found in growths of *Chara* or *Elodea* and on hard bottom. At 12 and 16 metres it was found among plant debris on top of soft clay.

INSECTA

PLECOPTERA

Perla sp. The full-grown nymphs of this stonefly were taken on exposed rocky shores at Jackson's Point and at Fox island. Fresh exuvia were found on the rocks at Beaverton on June 7, 1928, indicating roughly its time of emergence. In the active washing of waves on stony shores it appears to find a substitute for the running streams which are its natural habitat.

EPHEMEROPTERA

The following list includes the mayfly nymphs which occur commonly in the lake. The collection of nymphs has been identified by F. P. Ide of the University of Toronto. Complete identification is, of course, not yet possible without rearing experiments.

Ephemeridae
- *Hexagenia limbata occulata* Wlk.
- *Hexagenia bilineata** Say.
- *Ephemera simulans* Wlk.

Baetidae
- *Leptophlebia* sp.
- *Blasturus* sp.
- *Choroterpes basalis* Banks
- *Ephemerella* sp. (*bicolor* group)
- *Caenis* spp.
- *Baetis* sp. (near *propinquus*)
- *Centroptilum* sp.
- *Baetisca obesa* Say.

Heptagenidae
- *Ecdyonurus* sp.
- *Ecdyonurus* sp. (near *canadensis*)
- *Ecdyonurus tripunctata* Banks.

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*McDunnough, working on the genus *Hexagenia* on Sparrow lake, 20 miles down the Severn river from Lake Simcoe, has decided that no typical *H. bilineata* are present. He lists three species, *H. rigida* McD., *H. affiliata* McD. and *H. viridescens* Wlk. A form taken at Lake Simcoe resembles *H. viridescens*, although it has not been definitely identified as such.

Ecdyonurus frontalis Banks.
Ecdyonurus sp. (*fusca* group)
Heptagenia spp.
Heptagenia sp. (*maculipennis* group).

In the open water the mayfly nymphs found were of three groups, *Hexagenia*, two species, *Ephemera simulans* and *Caenis* spp. In the shore zone a great variety of forms occurs in more or less equal numbers, but showing preference for different types of shore.

Of the two burrowing genera, *Hexagenia* is the more abundant. It was taken on a great variety of bottoms from the soft clayey mud of the deeper water to sand, hard clay or mud and reeds of the inshore formations. Gravel and stone are the only kinds of bottom that it does not inhabit, and like the other open water forms, *Ephemera* and *Caenis*, it abounds in *Chara* beds. Its range covers the entire littoral and sublittoral zones and extends into the upper profundal where it is found living in the mud at depths as great as 21 metres. The swarming of *H. occulata* takes place early in July when enormous numbers of subimagos and adults attract the ciscoes of the lake to the surface for a period of ten days (page 156). The time of emergence of *Hexagenia bilineata* (or *viridescens*) is not accurately known, although a few subimagos were taken as early as June 15, in 1928.

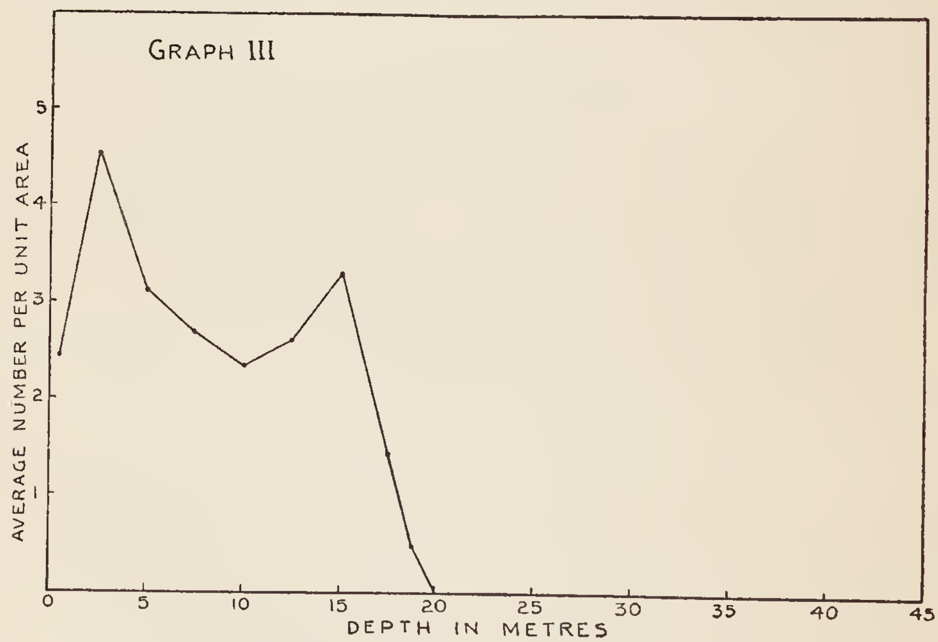
Ephemera simulans is less abundant and more limited in range than members of the genus *Hexagenia*. *Ephemera* is confined to the littoral and upper sublittoral, rarely occurring in depths of more than 9 metres. It is less frequently found in muddy bottom and shows a distinct preference for marly clay with *Chara* or a soft sand. *E. simulans* began to swarm on June 27, 1928, subimagos having been taken in large numbers at that time. They form a part of the swarms which attract the ciscoes during the first week of July.

Of the Baetidae, *Caenis* is much the most abundant and widest in distribution. It resembles *Hexagenia* in ranging from shore to 20 metres and inhabiting a variety of bottoms. *Ephemerella* is found on rocky and sandy shores but reaches depths of 2 or 3 metres if *Chara* beds are present. *Caenis* and

Ephemerella are interesting as "sprawling" types of nymphs, which live on the bottom in open water, in contrast with *Hexagenia* and *Ephemera* which are true burrowing forms and are quite at home in the muddy depths. *Leptophlebia* nymphs were found on sand or marl, often among *Chara.* The remaining Baetidae, including *Choroterpes, Baetis, Centroptilum* and *Baetisca,* were all found on exposed rocky shores, *Baetisca* inhabiting the most exposed places available.

The Heptagenidae are varied but are not particularly abundant in Lake Simcoe. Their depressed form adapts them to their habitat among stones or gravel on the wave-washed shores. With the exception of a few specimens of *Ecdyonurus* taken in a protected sandy bay, all the Heptagenidae were collected from such exposed rocky shores.

The distribution of mayfly nymphs as a whole is shown in graph III.



Graph III. The distribution of mayfly nymphs according to depth.

The maximum number found in the shore zone, 0 to 5 metre area, is due to the variety of the near-shore forms. A second maximum at 15 metres is due to the abundance of

large *Hexagenia* nymphs in the lower sublittoral and upper profundal. The decrease in numbers in the sublittoral is a common feature in the distribution of many groups of bottom organisms. The sublittoral is a transition zone between the littoral and the profundal. Having little distinct fauna of its own it is populated by a mixture of littoral and profundal forms, neither of which find it quite favourable, and the result is a small population as compared with the neighbouring zones.

The distribution of ephemerid nymphs in Lake Simcoe is quite unlike that found in Lake Nipigon. In the latter they are confined to the upper 10 metres while in Lake Simcoe the large Ephemeridae are plentiful between 10 and 20 metres.

As food for bottom-feeding fish, *Hexagenia* and *Ephemera* are the only important genera. *Caenis* is too small to be of much value and all the remaining species inhabit the littoral zone, which limits their usefulness as food for fish.

ODONATA

The dragonfly nymphs collected in Lake Simcoe were taken from the shore zone, 0 to 1 metres, with the exception of one specimen of *Didymops transversa* brought up from a depth of 3 metres near the mouth of the Black river. A small collection was submitted to Dr. E. M. Walker of the University of Toronto, who reports the following species:

Lestes rectangularis Say.
Enallagma boreale Selys
Enallagma exsulans Hagen?
Enallagma hageni Walsh
Ischnura verticalis Say.
Hagenius brevistylus Selys
Dromogomphus spinosus Selys
Boyeria grafiana Wmsn.
Basiaeschna janata Say.
Anax junius Drury
Didymops transversa Say.
Tetragoneuria cynosura Say.
(or *T. spinigera* Say.)

Protected bays with partly submerged vegetation are the preferred habitat for many of these nymphs. Such a bay is found between the Sand islands and Georgina island where a fine sandy bottom supports a moderate growth of *Scirpus*, *Nymphaea* and other rooted aquatics. A single collection from this habitat on May 29, 1927, contained numbers of *Enallagma boreale*, *E. exsulans*, *Hagenius brevistylus* and *Tetragoneuria cynosura*. On July 21, 1927, a similar habitat in the Narrows at Atherley yielded numbers of *Lestes rectangularis*, *Ischnura verticalis*, *Basiaeschna janata* and *Anax junius*. This distribution, *i.e.* very limited but abundant in suitable habitats, was characteristic of the whole group.

A single specimen of *Boyeria graphiana* and four of *Enallagma hageni* were collected from rocky shores at Big Cedar point.

No living specimens of *Dromogomphus* were collected, but three specimens were taken from the stomachs of small-mouthed black bass and yellow perch.

HEMIPTERA

The aquatic Hemiptera are not to be considered as true bottom forms since they swim and feed freely through the water of protected areas. Three common forms were collected in the weedy protected bays, *Lethocerus americanus*, *Notonecta* and *Corixa*. Apart from the occasional appearance of *Notonecta* and *Corixa* in the food of perch, the Hemiptera are of little interest in the ecology of the open lake.

NEUROPTERA

Sialis sp. The larvae of a small sialid, probably *S. infumata* New., were scattered over a wide range of depth and a variety of bottom. It was found from depths of 1.5 metres down to 19 metres with a maximum at 10 metres. Juday and Muttkowski found it ranging from 5 to 20 metres in Lake Mendota. It was, however, much more abundant in Mendota as indicated by an average of 10 individuals per square metre and a frequent occurrence in perch stomachs. In Lake Simcoe the average number is 2.2 per square metre and on only one occasion was it found in fish stomachs.

LEPIDOPTERA

Nymphula sp. The larvae of this small moth were found in the channel between Snake island and the mainland. A number of specimens were dredged up from a depth of 4 metres where the bottom was of clay and supported a scattered growth of potamogetons.

TRICHOPTERA

The caddis larvae are an important component of the littoral fauna and certain species penetrate the sublittoral zone to depths of about 10 metres. A selection of larvae was submitted to C. K. Sibley, of Clayton, Missouri, who has reported the following forms:

Hydroptilidae

Hydroptila sp. Two specimens were taken on stony shore.

Oxethira sp. A single specimen was collected from clay bottom in 4.5 metres of water.

Hydropsychidae

Hydropsyche sp. This form was common on stone or reeds, also on clay in depths of 1 to 2 metres.

Hydropsychodes analis Bks. Large numbers of this form were collected from stony shores.

Polycentropus sp. A single specimen was found in mud at 1.5 metres.

Sericostomidae

Helicopsyche borealis Hag. This form was very abundant on semi-exposed stony shore.

Phanopsyche sp. A few specimens of this genus were taken on sandy shores.

Molannidae

Molanna sp. *Molanna* is common on exposed sand or stones down to depths of 2 metres.

Leptoceridae

Leptocerus sp. This is one of the two caddis larvae that are found at considerable depths in Lake Simcoe. Frequent specimens were taken from

mud bottom at 6 to 17 metres, others from hard clay in 2 to 5 metres, and a few from stony shores.

Leptocerus uwarowii Kol. This species is less common than the last form. It is found at depths of 0 to 10 metres, usually on sand or gritty bottom, and was also frequent on the shore vegetation.

Oecetis sp. *Oecetis* is more abundant than *Leptocerus* sp., but not found deeper than 7 metres. It was taken from clay, marl or sand, but never from mud or rock bottom.

Setodes grandis Bks. Rare. This species was found on clay bottom 1 to 2 metres in depth.

Trianodes sp. Trianodes was collected from sandy bays with vegetation and occasionally on clay bottom down to 5 metres in depth.

Phryganeidae

Phryganea sp. A single specimen was found on clay bottom at a depth of 6 metres.

Phryganea interrupta Say. This form was not uncommon in sand or silt at the edge of *Scirpus* beds.

Limnophilidae

Limnophilus sp. This species was common on stones or wood debris.

Limnophilus rhombicus L.? A few specimens of this species were taken on sand among plant debris.

Halesus guttifer Walker. This species was found only on exposed stony shore.

Stenophylax scabripennis Rambur. This common species was taken on stone or sand shores with wood debris.

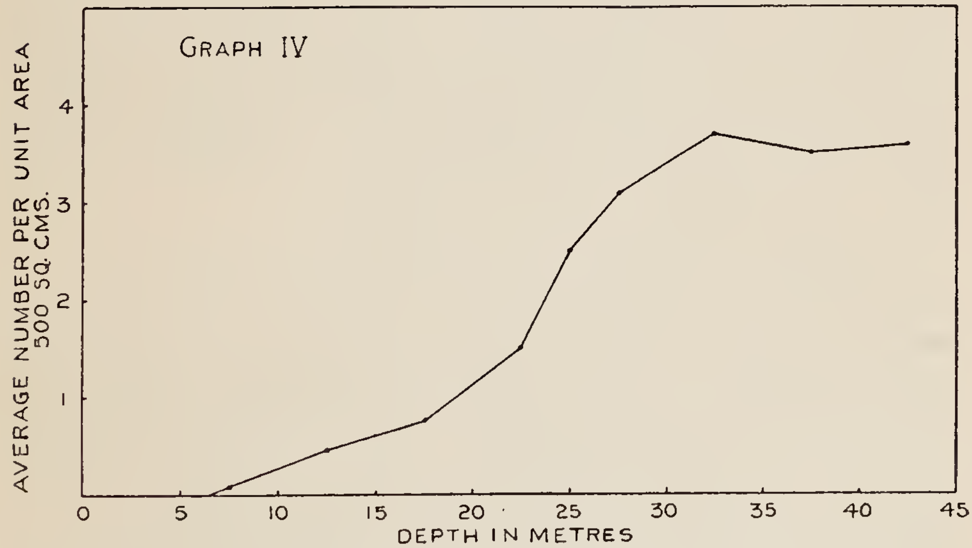
While the caddis larvae of the lake are as a whole shore forms, two species, *Leptocerus* sp. and *Oecetis* sp., extend into the sublittoral in large numbers. These species, with others of the family Leptoceridae, are occasionally found in the stomachs of whitefish, perch and bass, though never in large numbers.

DIPTERA

The Diptera of the lake belong mainly to the two families, Corethridae and Chironomidae. Occasional specimens of Tabanidae, Psychomyiidae, etc., have been collected from the shore zone in various parts of the lake. Such forms are abundant only in small, quiet bays and are not typical lake forms. We therefore confine our discussion to the two first-mentioned families.

Corethridae

Corethra sp. The larvae of *Corethra* are not true bottom-living forms since they can and do swim freely away from the bottom under certain conditions. Conversely they are not truly limnetic forms since at certain times they rest upon the bottom. We therefore include them in our study of the bottom fauna.



GRAPH IV. The distribution of *Corethra* larvae according to depth.

The distribution of *Corethra* larvae according to depth is indicated in graph number IV. Beginning in small numbers at 7 metres they increase slowly down to 20 metres. A more rapid increase is observed from 20 to 30 metres with a maximum abundance retained from that depth (30 metres)

into the deepest water. *Corethra* is definitely a profundal organism in Lake Simcoe.

In Lake Mendota, Juday and Muttkowski found a similar distribution. Lundbeck, in his studies of north German lakes, mentions *Corethra* as the only profundal species which had its maximum in the lower profundal, *i.e.* depths greater than 20 metres. In Lake Simcoe *Corethra* collected at depths of 7 to 20 metres were all from soft muddy bottom. In view of the fact that in the deep water where *Corethra* occurs most plentifully, the bottom is all muddy, it would appear that this type of bottom is partly responsible for the distribution of *Corethra.*

The abundance of *Corethra* in Lake Simcoe is small as compared with Mendota or the above-mentioned north German lakes. The average summer abundance of *Corethra* larvae in the profundal zone of Lake Simcoe is about 40 per square metre, a small population as compared with 16,000 per square metre in Lake Mendota. During three seasons of the investigation on Lake Nipigon, Adamstone found no *Corethra* larvae although specimens have since been taken from a nearby lake. The data suggest that larger lakes such as Simcoe and Nipigon are less favourable for the production of *Corethra* than smaller ones, e.g. Mendota.

Seasonal variation in the numbers of *Corethra* larvae due to their life cycle is an important factor in the study of their abundance. The numbers of *Corethra* in the profundal zone in Lake Simcoe vary from 38 per square metre in May to a minimum of 9 per square metre in late July and an increase to 42 per square metre in October. In November the number had risen to 70 per square metre. This situation is to be attributed to the fact that *Corethra* has its maximum emergence in late July and early August. A similar condition was observed by Juday on Lake Mendota, where he followed the numbers of *Corethra* at a deep-water station, 23 metres, over a period of two years. A graph in his paper of 1922 shows the seasonal variation in numbers of larvae per square metre. An extended maximum exists from October to May and falls to a sharply defined minimum in August. This minimum he

ascribes to the maximum emergence of *Corethra* which, as Muttkowski had recorded, took place between June 15 and August 20, with smaller numbers emerging as late as September 30.

Two features in the seasonal distribution of *Corethra*, larvae in Lake Simcoe have not been recorded from other lakes. In the 10-20 metre zone, where through the rest of the growing season the number of larvae average 2.3 per square metre, in July the numbers rise suddenly to 6.8 per square metre. If this result was due to encountering large swarms rather than to a general increase in numbers, the occurrence of such swarms in shallow water at this period is still unexplained. A second point was observed with reference to the abundance of larvae in May. The average abundance of 38 per square metre in the profundal zone was the result of 42 per square metre in the upper profundal and only 22 per square metre in the lower part of the zone, *i.e.* from 35-45 metres. This lowered occurrence in the last 10 metres was not found in the autumn distribution and is as yet quite unexplained. It is unlikely that the situation could have been the result of a scarcity of oxygen since the bottom oxygen at 40 metres ranged from 8.2 to 6.7 p.p.m. during May.

Corethra larvae are known to make nocturnal upward migrations. The statement made by Juday and others, that they lie on the bottom ooze during the daytime and swim away from it at night, was confirmed by horizontal tows taken at different depths in Lake Simcoe. The observations were made during June, 1928, off Thorah island. During the middle portion of the day no *Corethra* were taken more than 1 metre above the bottom. Tows taken at night showed their presence 6 to 8 metres from the bottom and on one occasion a swarm of larvae was encountered at the surface in a depth of 12 metres of water. Juday found that the immature larvae were always free swimming and that only mature forms lie on the bottom. The fact that in Lake Simcoe no young larvae were taken on the bottom may be regarded as partial confirmation of this observation.

Muttkowski describes the duration of the larval stage as six or seven weeks with a pupal life of one to three days. He suggests the possibility of three generations in one summer, winter larvae pupating in May, a second lot in July and the last generation in September. An exactly defined minimum abundance was found in late July in Lake Simcoe and in August in Lake Mendota. Since this minimum indicates the maximum emergence it is doubtful if the early and late generations are of any significant numbers.

Different investigators are not quite agreed on the food habits of *Corethra* larvae. An extensive study of the ecology of this form was made by Frankenberg (1915), who observed that they ejected undigested debris from their mouths after feeding. He suggests that *Cyclops* is the favourite food of *Corethra* and that the distribution of the larvae in deep water is determined by the abundance of *Cyclops*. Alsterberg (1924) and Lundbeck (1926) have both verified this relation in European lakes. Muttkowski (1918) states that they feed chiefly on the bottom ooze. He has observed them eating *Volvox* in shallow water.

In certain lakes *Corethra* larvae are important as fish food. Alsterberg (1926) mentions *Corethra* as a favourite food of fish and suggests that the distribution of fish in deeper water is sometimes due to the supply of this organism. In the deep water of Lake Mendota, Juday estimates the yearly crop of *Corethra* larvae at more than 100 kgm. dry weight per hectare, which is a large proportion of the total bottom fauna production. In these depths Muttkowski mentions that perch were frequently gorged with *Corethra* larvae and that bottom-feeding fish ate large numbers of them. In Lake Simcoe the number of *Corethra* larvae is much too small to make them an important source of food. They were found in stomachs of whitefish, sucker and perch, but only in negligible quantities.

Chironomidae

Chironomid larvae are characteristic and important members of the bottom fauna in fresh water lakes. In Lake

Simcoe they are the most abundant group of bottom organisms, forming 60 per cent. of the total population by number and 65 per cent. by weight. A collection of larvae was submitted to Professor O. A. Johannsen of Cornell University, who records the following genera and species:

Chironomus plumosus L.
Chironomus spp.
Chironomus subg. *Cryptochironomus*
Chironomus subg. *Microtendipes*
Tanytarsus spp.
Tanypus (*Ablabesmyia*) sp.
Procladius (sens. lat.)
Culicoides sp.

Chironomus plumosus L. *C. plumosus* is the outstanding species among the chironomid population. It is more numerous than any of the other groups of chironomid larvae and reaches the greatest size, being frequently over 25 mm. in length. In numbers it makes up one-quarter of all the chironomids in the lake and in weight some 35 per cent. of the total chironomid population.

The distribution of *C. plumosus* according to depth shows a scattered occurrence from 5 to 10 metres with an abundance from 10 to 45 and the maximum between 20 and 35 metres. It is definitely a profundal species, a conclusion which is confirmed by the fact that it occurs in 5-10 metres only in places where the bottom is soft and muddy, *i.e.* resembling that of the profundal. A very different distribution of *C. plumosus* was observed by Muttkowski in Lake Mendota. Here it was confined to the littoral area and in depths of more than 7 metres it was replaced by the other large species, *C. tentans*. Neither of these larger forms was present in Lake Nipigon where few chironomid larvae were more than 10 mm. in length.

No swarming of *C. plumosus* was observed on Lake Simcoe, the only adults being taken between September 6 and 14, 1926. Lundbeck, in the Plöner See, found the species emerging gradually during September and October. A very

different condition was observed by the author on Waskesiu lake in northern Saskatchewan. In this lake, *C. plumosus* swarmed on August 27, 1928. At the time several areas of 2 to 4 acres on the surface of the lake were completely covered with a heavy layer of pupae and newly emerged adults.

Chironomus plumosus appears to be well adapted to life in the deepest water with such aids to respiration as haemoglobin in the blood and the presence of both anal and ventral blood gills. These structural features are probably an aid to respiration, but they are by no means constant in all the chironomid larvae which frequent the deep water. Neither are these features limited to the deep-water species. Muttkowski emphasizes the absolute lack of any correlation between colour and oxygen supply. He found bright red species on shore and pale species in the deep water. Moreover, the coloration varies greatly within a single species. *C. plumosus* in Lake Simcoe was usually red, but sometimes yellow or greenish with no observable correlation between these colours and variation in depth or oxygen supply. In the final analysis it must be recognized that *C. plumosus* is a very resistant species, not only from its ability to live at great depths, but from its toleration of lowered oxygen supply and general pollution, as established by Richardson in his studies on the Illinois river (1921-25).

Chironomus spp. Members of the typical subgenus of *Chironomus*, other than *C. plumosus*, were not distinguishable in their larval form. Their total number is almost as great as that of *C. plumosus* alone. The distribution of the group is more or less uniform from shore to the deepest water and over sand and mud bottom. It is supposed that this situation is due to the grouping of a number of species with different habitats rather than to one or two very cosmopolitan species.

Chironomus subg. *Cryptochironomus*. The subgenus *Cryptochironomus* ranks fifth in numbers among the above-mentioned groups of chironomid larvae. They occur most frequently in the sublittoral zone, being present in practically every dredging between the depths of 5 and 15 metres. Some individuals were taken from the littoral zone chiefly in mud

or *Chara* beds and scattered individuals were found in the profundal zone to depths of 36 metres.

Chironomus subg. *Microtendipes.* Very few specimens were taken of this group and these all on hard bottom, sand or clay, with *Chara.* All individuals were found between depths of 3 and 7 metres. Lundbeck mentions *Microtendipes* as living near shore in summer and migrating towards deeper water with the onset of winter.

Tanytarsus spp. *Tanytarsus* was most abundant in 3 to 5 metres with a moderate occurrence down to depths of 30 metres. It is slightly more abundant than *Cryptochironomus* but less regular in its occurrence.

Tanypus (*Ablabesmya*) sp. Small numbers of this form were taken at irregular intervals between depths of 1 and 10 metres. Practically all the specimens were from sand bottom.

Procladius (sens. lat.). The procladius group is abundant in Lake Simcoe, being surpassed only by the typical subgenus *Chironomus*. *Procladius* resembles the latter group in distribution, being cosmopolitan both as to depth and type of bottom. Almost uniform numbers are found from 2 to 45 metres. In the lower profundal it equals *C. plumosus* in numbers but is of much less consequence because of its smaller size.

Culicoides sp. *Culicoides* was the only genus of the Ceratopoginae taken during the survey. It was frequent in the littoral zone, 1 to 4 metres, while scattered individuals were found as deep as 8 metres. It is therefore the only littoral form among the chironomid larvae of Lake Simcoe. The habit of swimming freely in the water provides a marked contrast between this form and the other chironomid larvae which have the tube-building habit. Lundbeck considers it as one of the active migrants among the bottom fauna.

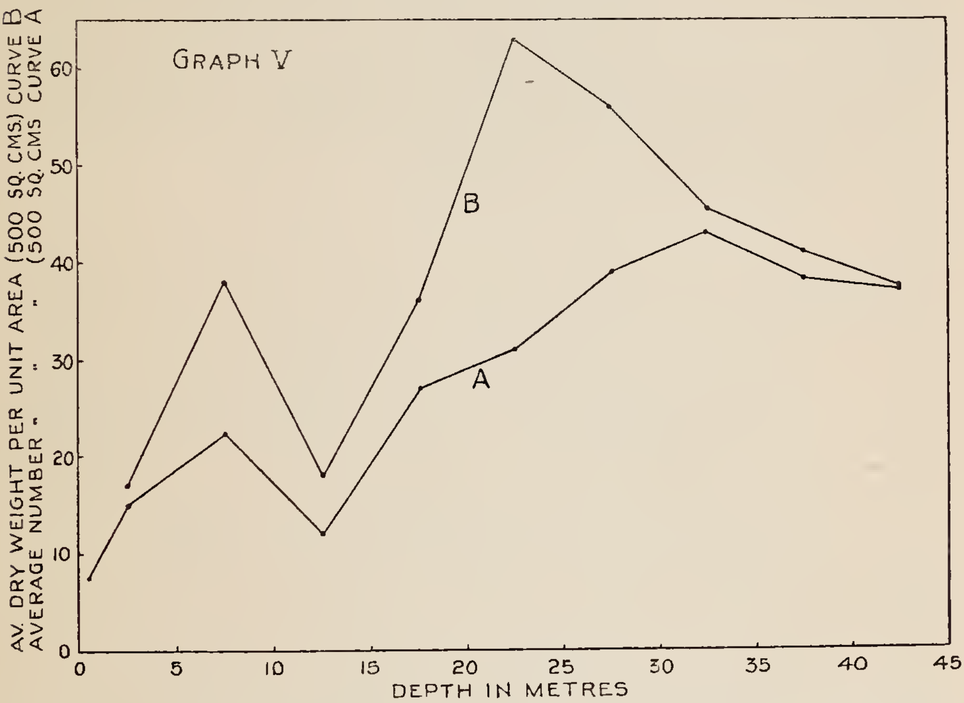
The total chironomid population of Lake Simcoe is made up of the above groups in the following proportions, *C. plumosus* 27 per cent., *Chironomus* spp. 27 per cent., *Procladius* 18 per cent., *Tanytarsus* 12 per cent., *Cryptochironomus* 10 per cent., *Tanypus*, *Microtendipes* and *Culicoides* together 6 per cent.

A noticeable feature of the chironomid fauna of Lake Simcoe is the variety of forms present in the deeper water. In Mendota, Juday found only two species, *C. tentans* and *Protenthes choreus*, the latter present only in small numbers. In the deep water of many north German lakes Lundbeck found two forms, *C. plumosus* and *C. libeli-bathyphilus* and frequently just one of these was at all numerous. In the deep water of Lake Simcoe, *C. plumosus* is abundant, but not more so than *Procladius*, while at least one other species of *Chironomus* is frequent down to depths of 35 metres. Added to this, *Cryptochironomus* and *Tanytarsus* both penetrate the deep water in small numbers. Lake Simcoe is subject to a lesser stratification than the other lakes in question and in consequence it seldom suffers a great deficiency of bottom oxygen. It may be for this reason that these varied forms are allowed to penetrate the deep water of Lake Simcoe, while in other lakes the scarcity of oxygen prevents their so doing.

The distribution of the chironomid population as a whole is shown in graph number V. Curve *A* indicates the numerical distribution of larvae according to depth. From this graph it is immediately evident that the bulk of the chironomid fauna is in the profundal zone. At the minor maximum, 7.5 metres, the numerical abundance is only half that of the maximum at 37.5 metres. The minimum observed at 12 metres in the lower sublittoral zone is of frequent occurrence in the depth distribution of bottom organisms. The sublittoral zone is a transitional region between the littoral and the profundal. Since it has little distinct fauna of its own it is populated by strays from the neighbouring zones. Sublittoral conditions are not favourable for either of these groups with the result that the population in this region is less thriving and smaller in quantity than in either the littoral or the profundal.

From curve *B*, showing the distribution of chironomid larvae by weight, it is obvious that the maximum weight production does not coincide with the maximum number of larvae. The former was at 22.5 metres while the maximum number was at 32.5 metres. In other words the larvae at 22

metres were larger than those in the deeper water. This condition has already been met with in another form since it was observed that *C. plumosus*, a large form, was abundant between 20 and 30 metres. Observations of the fishing carried on in Lake Simcoe indicate that bottom-feeding fish are rarely found feeding at depths greater than 30 metres. It is therefore important to know that the greatest supply of chironomid larvae, a staple food, is located between 20 and 30 metres where it is available for bottom-feeders.



Graph V. The distribution of chironomid larvae,—A numerically, B by weight in mgms.

In comparison with *Corethra* larvae it is observed that while both forms have their maximum numbers in the lower profundal, chironomid larvae differ in having their maximum weight in the upper profundal. Lundbeck mentions *Corethra* as the only profundal species with its maximum production in the lower profundal, which is essentially the same condition that we find in Lake Simcoe.

The average summer population of chironomid larvae in Lake Simcoe is about 590 per square metre over all depths. In deep water, 20 to 45 metres, the average is 676 per square metre and in depths of less than 20 metres the average is only 250. This may be considered a fauna of moderate density. Lake Mendota has more than twice as many as this and most of the small German lakes studied by Lundbeck have even greater chironomid populations. Lake Nipigon, on the other hand, was much poorer in chironomids, not only on a basis of numbers per unit area, but also on a basis of the relative proportion of chironomid larvae in the total fauna. The difference is even greater when we compare the total weight per unit area or the weight of chironomids as a percentage of the total population. Table 3 indicates the marked difference in the chironomids of the two lakes.

TABLE 3. A comparison of the chironomid larvae in Lake Simcoe and Lake Nipigon.

	Average number of chironomid larvae per square metre.			Chironomids as percentage of total bottom fauna.		Average dry weight of individual larvae.
	0-20m.	20m.—max. depth	All depths	Numerically	By weight	
Lake Simcoe..	250	676	590	65%	63%	1.490 mgm.
Lake Nipigon.	295	80	138	33%	7%	0.114 mgm.

In Lake Simcoe the bottom fauna of deep water is made up largely of chironomid larvae, while in Lake Nipigon the chironomid larvae are far surpassed by the deep-water amphipods. The data would tend to confirm the general observation that larger lakes have increasingly smaller chironomid populations.

The question arises as to whether 590 chironomid larvae per square metre (the average population for all depths from

May to October, inclusive) is a correct representation of the chironomid fauna of Lake Simcoe. During the summer chironomid larvae, pupate, emerge and are lost to the lake. The adult deposits eggs in the lake which give rise to the next year's generation. It is obvious that this cycle must cause a considerable variation in the number and size of chironomid larvae present at any given season. It is desirable to know the magnitude of this variation and the time of maximum and minimum quantities. The most complete data on this subject are the result of the excellent work carried on by Thienemann and Lundbeck in lakes of northern Germany. Lundbeck followed the monthly variation in size and number of chironomid larvae in a part of the Plöner See for two years. His results indicate the increase in number and quantity of chironomid larvae due to reproduction and growth. They also show the decrease which results from mortality (being eaten, etc.) and to the emergence of adults. The summer's hatch of chironomid larvae brought about a great increase in numbers. A period of rapid growth during the autumn resulted in a maximum abundance in January. From that time the mortality due to being fed upon by fish, etc., brought about a decrease which reached a minimum when the greatest emergence of adults took place. These maximum and minimum numbers were the integrated result of variation in different species. The deeper waters of the Plöner See were populated by *Chironomus plumosus* and *C. libeli-bathyphilus*. The emergence of *C. plumosus* was not sharply defined, the last of the old generation remaining for several weeks after the first of the new generation of larvae had appeared. *C. libeli-bathyphilus*, on the other hand, emerged quickly during the latter part of May.

It is now possible to return to the question of the validity of our determinations of the chironomid fauna of Lake Simcoe. The variety of species living in the deep water of Lake Simcoe prevents the appearance of a definite minimum since the periods of emergence do not coincide. We must remember, however, that samples taken through the summer season include the periods at which all forms emerge and the later

periods at which all the larvae are immature. In other words our samples from May to October include the minimum occurrence and miss the maximum which, as Lundbeck has shown, exists at the end of the autumn growth. As a result, the estimate of the chironomid fauna must be lower than the yearly average for the lake.

Chironomid larvae are a staple food for bottom-feeding fish. In Lake Simcoe the Mollusca and Ephemeridae form a large part of the diet of such fish with the result that chironomid larvae are less important than usual. This subject will be fully discussed in Part II as will a further ecological function of the chironomid larvae, namely, their activity in converting organic detritus from the bottom ooze into food for other members of the lake fauna.

COLEOPTERA

The aquatic beetles in the adult form are hardly to be considered as part of the bottom fauna. The larvae are also free-swimming, but feed partly on bottom with the other members of the shore fauna. They are limited to protected situations and take little part in the ecology of the open waters in which we are chiefly interested.

Dytiscidae

Coptotomus sp. Larvae of this beetle were taken near the mouths of creeks among vegetable debris and from depths of 1 to 2 metres.

Dytiscus sp.

Thermonectes sp.

The larvae of these forms were found together in protected weedy bays, usually over a sand bottom.

Gyrinidae

Several small gyrinids were collected from protected shores in different parts of the lake. They have not been identified further.

Parnidae

Psephenus lecontei Lec. The limpet-like larva of this beetle is a constant inhabitant of the stony shores. It is the most abundant coleopterous larva in the lake. On wave-washed stony shores it was almost invariably found associated with two other bottom forms, a caddis larva *Hydropsychodes analis*, and a small leech *Dina parva*.

Elmis sp. An unusual occurrence of this form was noted in Kempenfelt bay on May 22 when a single specimen was taken from mud bottom at a depth of 23 metres.

ARACHNIDA

HYDRACARINA

The abundance of water mites in Lake Simcoe is indicated both by the number taken in dredging and the much larger number found in fish stomachs. The material has been examined by Dr. Ruth Marshall of Rockford, Illinois, and has been incorporated in her paper on Canadian Hydracarina (Marshall, 1929). She records twenty-one species, four of which are new, from the Lake Simcoe material.

Limnochares aquaticus (L.). Common.

**Eylais abitibiensis* Mar. A single specimen.

Eylais infundibularis Koen. A single specimen.

Lebertia porosa Thor. Commonly taken in whitefish stomachs.

**Lebertia ontarioensis* Mar. Specimens from bottom 20 metres and from whitefish stomachs.

Limnesia undulata (Müll.). From mud bottom in 8 metres of water and common in whitefish stomachs.

Limnesia histrionica wolcotti Piers. Taken at depths of 4 to 6 metres and from stomachs of whitefish and cisco.

Limnesia maculata americana Piers. Four specimens from different parts of the lake.

Species marked with an asterisk(*) are newly described in the above-mentioned paper.

Limnesia cornuta Wol. Rare species, one specimen only at depth of 1 metre.

Limnesiopsis anomala (Koen.). Common at moderate depths, e.g. 5 metres.

Hygrobates longipalpis (Herm.). Common in a variety of locations, near shore, on bottom in 5 metres and from whitefish stomachs.

Unionicola crassipes (Müll.). Fourteen specimens from a single whitefish stomach.

Neumania semicircularis Mar. Three scattered collections, one from bottom in 23 metres of water.

Neumania ovata Mar. A single specimen from 6.5 metres.

Piona constricta (Wol.). A single specimen.

Piona pugilis (Wol.). Four individuals from depths of 2 to 5 metres.

Piona turgida (Wol.). Five specimens from a single dredging.

**Piona interrupta* Mar. Single specimens taken at seven different places.

**Acercus diversus* Mar. One specimen taken from a depth of 2 metres.

Mideopsis orbicularis (Müll.). Common.

Arrhenurus serratus Mar. A single specimen.

It is noteworthy that the largest genus, *Arrhenurus*, is represented by a single specimen of the species *A. serratus*. Although water mites are not sufficiently abundant to form an important source of food, it was observed that they were present in one-third of the whitefish stomachs examined and as many as 30 individuals were frequently taken from a single stomach. The water mites found in stomachs of suckers and perch were few as compared with those taken from the whitefish.

Species marked with the asterisk(*) are newly described in the above-mentioned paper.

MOLLUSCA

In the bottom fauna of Lake Simcoe the Mollusca are well represented in variety, but scanty in numbers as compared with other lakes. A collection has been submitted to Dr. Bryant Walker, who has identified the Gastropoda, and to Dr. V. Sterki, who determined the Sphaeriidae.

GASTROPODA

Owing to the large number of species it was considered advisable to condense the data as to distribution and abundance of Gastropoda into the following table.

TABLE 4. The Gastropoda of Lake Simcoe.

Species	Abundance	Range and usual habitat
	A = abundant C = common R = rare	Species inhabits shore only (0-1 m.) unless otherwise stated.
1. *Lymnaea stagnalis appressa* Say....	C	Shores of protected bays in *Scirpus*.
2. " *haldemani* Desh.........	R	Shores of protected bays with vegetation.
3. " *humilis modicella* Say....	R	Debris by river's edge.
4. " *obrussa* Say.............	C	Shore to 5 m., sand and vegetation.
5. " " *decampi* Say....	R	Shore only, sand or gravel.
6. " *galbana* Say.............	C	Shore to 10 m., protected.
7. " *palustris* Müll...........	R	Shore only, among *Typha* or *Scirpus*.
8. " *catascopium* Say..........	A	Widely distributed, exposed or weedy shore.
9. " *emarginata* Say...........	C	1-10 m., clean sand bottom and *Chara*.
10. *Planorbis antrosus* Con...........	R	Exposed shore also in *Scirpus*.
11. " " *striatus* Baker...	C	0-10 metres.
12. " " *portagensis* Baker	R	Shore, with vegetation.
13. " *altissimus* Baker........	C	Shore to 5 m.
14. " *campanulatus* Say	A	Widely distributed, shore to 10 m.
15. " *deflectus* Say...........	A	Exposed 0-5 m., stone. vegetation.

TABLE 4—*Continued*

Species	Abundance A = abundant C = common R = rate	Range and usual habitat Species inhabits shore only (0-1 m.) unless otherwise stated.
16. " *exacuous* Say	C	Shore, vegetation.
17. " *hirsutus* Gld	C	Shore, mud, near creek.
18. " *parvus* Say	C	Shore to 10 m., near vegetation.
19. " *trivolvis* Say	C	Protected shores with vegetation.
20. *Physa ancillaria* Say	A	0-10 m., exposed sand and rock shore.
21. " " *magnalacustris* Wlk.	R	Less exposed shores.
22. " *elliptica* Lea	R	Shore, stones.
23. " *gyrina* Say	C	Shore to 10 m., swampy creek.
24. " *integra* Hald	C	Exposed shores.
25. *Ferrissia* sp.?	R	Muddy shore.
26. " *fusca* C.B.Ads	R	Mud and marsh.
27. " *parallela* Half	C	Shore to 5 m., protected bay.
28. *Campeloma decisum* Say	A	Shore to 8 m, cosmopolitan.
29. *Amnicola emarginata* Kust	C	Shore to 25 m., mud.
30. " *limosa* Say	A	Shore to 35 m., sand or mud.
31. " " Say. var?	R	Shore to 10 m., mud.
32. " *lustrica* Pils	A	Shore to 35 m., mud or shore vegetation.
33. " *walkeri* Pils	R	Shore.
34. " *winkleyi* Pils	R	Shore to 10 m., vegetation.
35. " *winkleyi mozleyi* Wlk	R	Debris at water level.
36. *Paludestrina* sp	R	Shore to 3 m., marshy.
37. *Valvata sincera* Say	A	Shore to 35 m., mud or sand.
38. " " *nylanderi* Dall	C	Shore to 20 m., sand.
39. " *tricarinata* Say	A	Shore to 35 m., cosmopolitan.
40. " " *perconfusa* Wlk.	A	Shore to 10 m., mud or sand.

In addition to the forty species listed above, several semi-aquatic and terrestrial forms were found at the water's edge.

Succinea retusa Lea. Two living specimens of this species, which were collected from a depth of 6 inches of water in a muddy bay, may have been washed in from shore.

Carychium exiguum Say., was found in rotten wood, partly submerged.

Zonitoides nitidus Müll. Frequents the water level in *Typha* beds.

Shells of the land forms *Helicodiscus parallelus* Say. and *Polygyra albolabris* Say., taken at depths of 2 and 3 metres and 100 metres from shore, had probably been swept out by the current from a nearby river.

A comparatively small number of the species occurring in the lake are able to penetrate to any considerable depth. Most of the species of *Valvata* and *Amnicola* are found down to depths of 20 or 30 metres. A few species of *Planorbis*, *Physa* and *Lymnaea* reach depths of 10 metres, but the greater number of species are confined to the shore zone. As a result of this distribution we find *Amnicola*, *Valvata* and *Physa* constituting the bulk of the molluscan food of the lake fish.

PELECYPODA

The following pelecypods have been collected in Lake Simcoe during the course of the investigation. The list of Sphaeriidae is probably incomplete since the collection identified by Dr. Sterki included only those specimens taken during the first season.

Lampsilis luteolis Lamark. Of the two larger mussels in the lake *L. luteolis* was the more common. Its preferred habitat is a soft sand bottom in depths of 1 to 3 metres of water and often in the neighbourhood of *Scirpus* beds.

Anodonta grandis Say. This species was distributed very much like *L. luteolis*, the only noticeable difference being a greater abundance of *Anodonta* in protected situations. Some very large specimens taken among the reeds in Smith's bay resembled the variety *footiana*, but further collections revealed a complete intergrading series.

Unio complanatus Solander. Since the only specimens of this species were taken at the mouths of creeks and rivers it is somewhat doubtful whether it should be included as an inhabitant of the lake.

Sphaerium crassum Sterki. This is a large species, both abundant and widespread.

Sphaerium exmarginatum Prime. Common on sandy bars and among *Chara.*

Sphaerium sulcatum Lamark. A large form common in sand or mud.

Sphaerium stamineum Conrad. Small numbers found on sand shores.

The genus *Sphaerium* is mostly confined to the upper eight metres and is most abundant on sand or stiff clay, in contrast with the smaller, mud-living members of the genus *Pisidium*, which are abundant in the deep water.

Pisidium adamsi Prime. form? A rare species found in shallow water.

Pisidium compressum Prime. This is probably the most abundant species of *Pisidium* in Lake Simcoe. It was taken in large numbers from mud and sand bottom, from shallow and deep water, and from various parts of the lake. In whitefish stomachs it was as common as *P. scutellatum.*

Pisidium pauperculum Sterki. This small form is found in deep water and frequently occurs in stomachs of whitefish.

Pisidium pauperculum nylanderi Sterki. Common in deep water.

Pisidium scutellatum Sterki. Very abundant and ranging from 3 to 40 metres in depth.

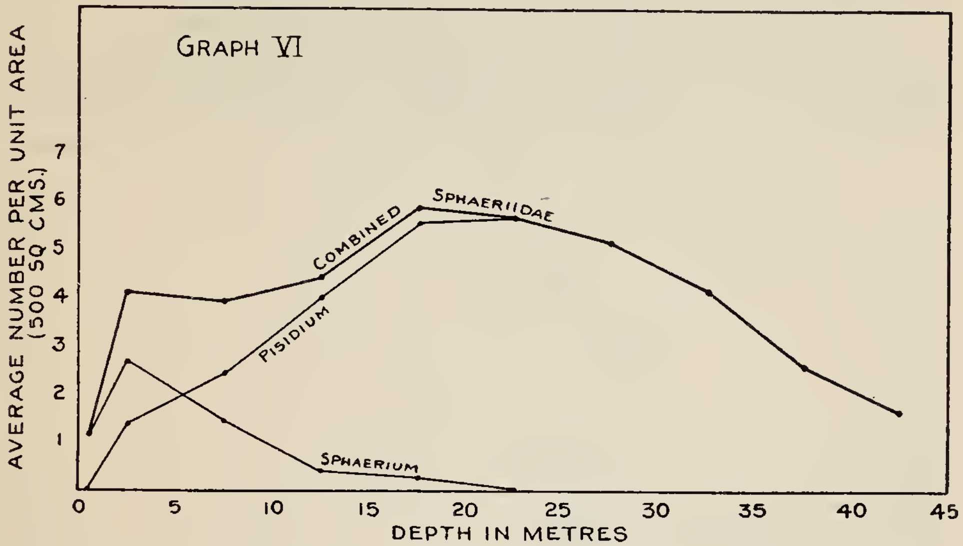
Pisidium variabile Prime. Abundant, especially on sand at moderate depths.

Pisidium vesiculare Sterki. This is not a common species, most of the specimens being found in whitefish stomachs.

Pisidium walkeri Sterki. Rare, found in mud along with *P. compressum.*

Graph number VI indicates the distribution of Sphaeriidae according to depth. The population is fairly constant

through the first 10 metres, but rises in the lower sublittoral and upper profundal to a maximum at 20 metres. From this point it decreases regularly to a minimum on the deepest bottom. The Sphaeriidae are peculiar in being the only group of bottom organisms in Lake Simcoe which shows no decrease in numbers in the sublittoral zone.

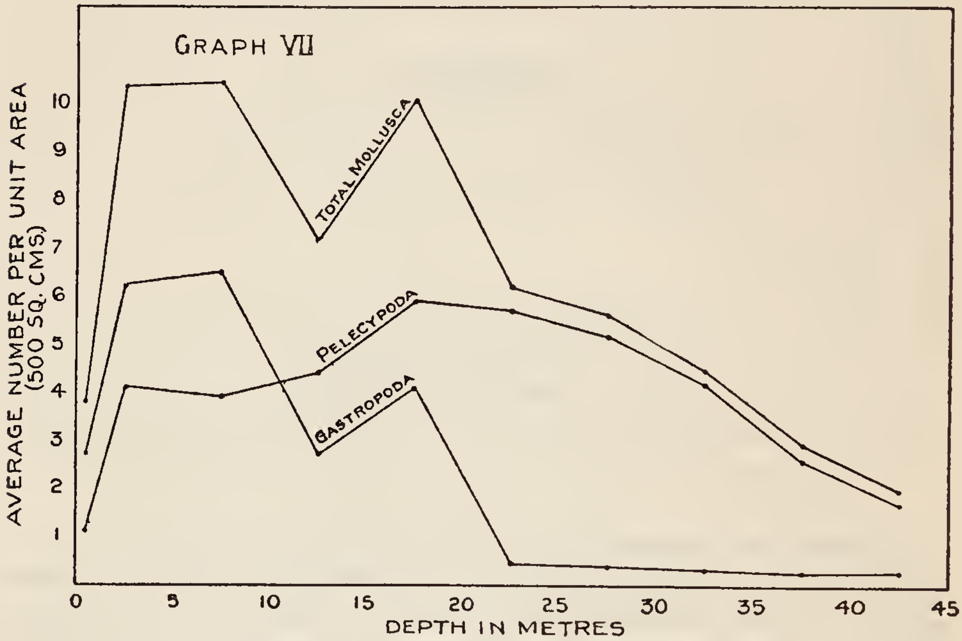


GRAPH VI. The distribution of *Sphaerium* and *Pisidium* separately and combined.

When we consider the distribution of the two genera which constitute the group, we see that *Sphaerium* decreases rapidly throughout the littoral and sublittoral zones, from which region it dwindles to disappear completely at 22.5 metres. *Pisidium* shows an unusually symmetrical distribution from a minimum at the shore to a maximum exactly halfway down (22.5 metres) and a second minimum in the deepest water. The dredging data indicate that several species of *Pisidium* range alike from 5 to 40 metres with equal numbers on sand and mud bottom. This general distribution, together with the absence of the usual decline in numbers at the sublittoral region, would indicate that the members of the genus *Pisidium* are little affected by the factors which usually control depth distribution. It is possible that

from shore to 20 metres they suffer less and less from food competition with the littoral and sublittoral bottom organisms belonging to other groups. These latter forms, decreasing from the shore to the greater depths, may allow these molluscs to increase. From 20 metres to 45 metres some factor directly dependent on depth causes a steady decrease in the numbers of the *Pisidium* group.

Graph VII includes the distribution curves for Gastropoda and Sphaeriidae, as well as the combined curve representing the total mollusc population, with the exception of



GRAPH VII. The distribution of Gastropoda and Sphaeriidae separately and combined.

the larger mussels *Lampsilis* and *Anodonta*. From shore to 10 metres the gastropods outnumber the Sphaeriidae, but, unlike the latter, the gastropods show a marked decrease in the sublittoral zone. After a slight increase between 15 and 20 metres, the gastropod population falls off to a low but constant number which persists into the deepest water. This part of the curve, 25-45 metres, is altogether due to the small numbers of *Amnicola* and *Valvata* which inhabit the deepest water.

The combined curve representing the total molluscan fauna, has the sublittoral minimum impressed upon it by the gastropods, while in the deeper water it follows the pelecypod distribution since they greatly outnumber the gastropods at depths of more than 20 metres.

In different areas of the lake the molluscan population varies considerably. A minimum variation exists in the deep water where we have few species and relatively constant living conditions. In the shallow water more varied conditions of bottom material, water movements and food supply result in a corresponding variation in the molluscan fauna. In general the eastern and southern parts of the lake are shallower and support a larger number of molluscs. The richest fauna observed was in an area of 5 square miles between Georgina island and the mainland. This large bay is protected on the east by Duclos point and on the west by the Sand islands. The depth of the water in the area is seldom greater than 5 metres and in many places shallow bars approach the surface. The bottom is covered with sand, silt or shell marl and the abundance of shell marl testifies to the magnitude of the molluscan population. In dredging series V an area of at least five acres was encountered in which dead shells of Sphaeriidae and Gastropoda covered the bottom to depths of 1 to 2.5 inches. The shells were more or less broken and mixed with a small quantity of silt. In this and several other parts of the lake the dead shells were so numerous as to make the separation of living molluscs from a dredging a very lengthy operation.

In the sublittoral region of Lake Simcoe we find no definite "shell zone." In Lake Mendota, Muttkowski found a distinct shell zone between 6 and 8 metres, similar to that described by various authors as existing between depths of 6 and 12 metres. It would appear that the conditions in large lakes such as Nipigon and Simcoe are not favourable for a great production of Mollusca and accumulation of shells at this depth.

Data on the distribution of molluscs in large lakes are relatively scarce. Adamstone has studied the problem thor-

oughly in Lake Nipigon. The two lakes, Simcoe and Nipigon, have almost nothing in common in the distribution of their molluscs. The gastropods of Lake Nipigon were confined to the upper 10 metres, while in Lake Simcoe they were numerous down to 25 metres and extended in small numbers into the deepest waters. The pelecypods of Lake Nipigon were most abundant in the first 4 metres with a minimum of 45 metres and a secondary increase below that depth. In Lake Simcoe the maximum was in middle depths, 20-25 metres, with decreasing numbers towards shallower and deeper water. The factors limiting this distribution have been suggested on page 65.

That the molluscs of Lake Simcoe are an important source of fish food will appear in Part II. Among the bottom-feeding fish, particularly the whitefish, the molluscs eaten constituted about one-quarter of their total diet. Of this molluscan diet the Sphaeriidae (chiefly *Pisidium*) make up 55 per cent., *Valvata* and *Amnicola* 35 per cent., *Physa* and *Planorbis* the remaining 10 per cent.

THE MICROFAUNA OF THE BOTTOM LAYERS

The microfauna is a vital link in the food circulation of the lake and in many respects is as important as the larger organisms, although the difficulty of sampling microfauna has had the effect of keeping its nature more or less obscure. In Lake Simcoe two methods of sampling were employed. The heavy sampler, as described on page 23, was used to bring up an undisturbed core of bottom material with the water immediately above it still in place. The advantage of the apparatus was that it brought up a known area, 71.3 sq. cm., of bottom in such a condition that the various horizontal strata and the water immediately above it could be examined separately. The ooze sucker (page 24) was useful in making qualitative samples of the upper ooze layer.

Of the twenty samples examined ten were taken from depths of 20 to 45 metres, five between 10 and 20 metres, and five between 3 and 10 metres. The observations were made

between May 9 and June 20, some in Kempenfelt bay and some in the open lake off Thorah island. Eight of the samples were taken with the ooze sucker and the remainder with the heavy sampler.

The following table summarizes the analyses of these twenty samples.

TABLE 5. Showing list of microfauna, occurrence at different depths and frequency of occurrence in twenty samples.

Microfauna	Depth distribution			No. of samples in which specimen occurred out of 20 examined
	2-10m.	10-20m.	20-45m.	
PROTOZOA				
Rhizopoda				
Amoeba sp	+	+		3
Arcella spp	+	+	+	11
" *vulgaris* Ehr	+		+	8
Campascus cornutus Leidy		+		2
Codonella sp			+	1
" *cratera*	+	+	+	8
Cyphoderia ampulla Ehr		+	+	9
Difflugia sp	+		+	4
" *globulosa* Duj			+	2
" *lobostoma* Leidy			+	6
" *pyriformis* Perty	+	+	+	10
Hyalosphaenia sp		+		2
Nebela sp		+	+	3
Mastigophora				
Anisonema sp	+			11
Euglena sp	+		+	8
Heteronema sp		+		1
Trachelomonas sp	+			3
Minute flagellates?	+	+	+	14
Ceratium sp. cysts		+	+	6
Ciliata				
Bursaria sp	+			3
Chilodon sp	+			1
Chilodonopsis sp	+			2
Colpoda sp			+	7

TABLE 5—*Continued*

Microfauna	Depth distribution			No. of samples in which specimen occurred out of 20 examined
	2-10m.	10-20m.	20-45m.	
Ciliata				
Heteromita variabilis Stokes		+		2
Holophrya sp	+		+	9
Lionotus sp	+			1
Loxophyllum sp			+	1
Nassula sp		+	+	4
Oxytricha sp	+	+	+	11
Paramoecium bursaria Ehr			+	6
" *caudatum* Ehr	+			2
Spathidium sp			+	1
Spirostoma sp			+	5
Stylonichia sp		+	+	10
" *mytilus* Müll			+	3
Urostyla			+	1
Minute ciliates	+		+	12
TURBELLARIA				
Mesostoma sp	+		+	5
Planaria sp	+	+		6
NEMATODA				
Minute unidentified	+	+		4
OLIGOCHAETA				
Nais sp	+			2
Stylaria sp		+	+	5
ROTIFERA				
Brachionus sp			+	2
Diaschiza sp	+			1
Dinocharis tetractis Ehr	+	+		7
Diplois sp	+			2
Keratella cochlearis var. *tecta*	+	+		4
Monostyla lunaris Ehr		+	+	5
Philodina sp	+	+	+	9

TABLE 5—*Continued*

Microfauna	Depth distribution 2-10m.	10-20m.	20-45m.	No. of samples in which specimen occurred out of 20 examined
CRUSTACEA				
Cladocera				
Sida crystallina (Müller)........		+	+	5
Daphnia longispina var. *hyalina* (Leydig)..................	+		+	3
Illyocryptus sp..................	+	+	+	8
Acroperus harpae Baird...........		+		2
Alona quadrangularis Müller......	+	+	+	8
Eurycercus lamellatus (Müller)....	+	+	+	11
Camptocercus rectirostris Schroedler.	+	+		4
Chydorus sphaericus (Müller)......	+	+	+	7
Copepoda				
Cyclops sp......................	+	+	+	8
Canthocamptus sp...............	+		+	5
Nauplii........................			+	2
Ostracoda				
Candona spp....................	+	+		4
Limnocythere spp...............	+			2
Unidentified spp.................	+	+	+	10
GASTROTRICHIA				
Chaetonotus sp.................	+			2
TARDIGRADA				
Macrobiotus....................	+	+		
HYDRACARINA				
Lebertea ontarioensis Mar.........			+	1
Neumania semicircularis Mar.....			+	2
" *ovata* Mar...........	+			1

The division of bottom organisms into macro- and micro-forms is a necessary distinction for convenience in field work but it is quite arbitrary. In some cases forms of intermediate

size have been included in both lists (Cladocera) and a few groups such as the oligochaetes and nematodes are represented in both macro- and microfauna. The above list of micro-organisms is necessarily quite incomplete, due to the small number of samples and to the difficulty of identifying some of the minute forms.

The greatest number of Protozoa are recorded from the 20-45 metre zone. This must not be taken as indicating a greater variety of Protozoa in the deep fauna since the number of samples taken in this area was twice that taken in the shallower zones. In the case of minute flagellates and ciliates the numbers were actually greater in shallow than in deep water.

The available data from Lake Nipigon deal only with the microfauna of the shallow water. Bigelow (1928) describes the forms living in the "inshore bottom systasis." Several of the rhizopod Protozoa are common both in Lake Simcoe and Lake Nipigon as are some of the ooze-living Cladocera. Of the Rotifera, only two forms, *Monostyla lunaris* and *Philodina* sp., were found in both lakes. Bigelow distinguishes between the organisms of the "ooze film cenosis," *i.e.* organisms living right in the ooze and the "associated ooze film cenosis", made up of organisms which swim about near the ooze and are dependent upon it for food. In the samples from Lake Simcoe the division is less distinct. Some of the Cladocera taken in the ooze are known to swim freely away from it, but any absolute division into two groups would be very difficult.

Of thirty-three Protozoa listed from the bottom of Lake Simcoe, fourteen were found by Kofoid (1896) on the bottom of Lake Michigan. Smith (1893) mentions six species taken in dredgings from Lake St. Clair, only one of which was found in Lake Simcoe.

The substrate on which the microfauna is found is worthy of mention, in particular the ooze bottom of the deeper water. In the profundal zone the bottom is composed of fairly constant proportions of mineral matter and organic detritus of plant and animal origin. In the littoral and sublittoral zones the proportion of mineral matter is higher and more variable, since in this area we find bottom of pure sand, stone, hard

clay, marl or combinations of these materials. The disturbing influence of water movements hinders the accumulation of soft ooze and organic debris in these upper zones. The profundal ooze has been examined more fully, partly because of the scarcity of previous observations in this field, and partly because of its comparative uniformity in composition.

The materials which compose the substrate in the profundal zone are as follows:

Mineral matter—Including particles of clay and silt with occasional sand grains and mollusc shells.

Organic matter (*or detritus*)

1. Plant debris:
   (*a*) Arising from the higher plants, aquatic or land, and including leaf particles, woody fragments and coniferous pollen.
   (*b*) Originating from the phytoplankton,—algae of various kinds, diatoms being most conspicuous.
2. Animal debris—chiefly planktogenous in origin, including husks of Entomostraca and Protozoa, fragments of dead bottom-living animals and fish bones. In Lake Simcoe *Bosmina* shells were the most noticeable representatives of this group.
3. Organic material not recognizable as of plant or animal origin. Mostly coprogenous, *i.e.* modified by passing through the alimentary tracts of bottom organisms such as oligochaetes and chironomid larvae.

The vertical distribution of these constituents in the various bottom layers may be considered from the surface layer downwards.

Layer A. A very thin film, 0.5 mm., which is not always present, is distinguished by its brownish or yellowish colour. It is composed of a flocculent organic material and the colour appears to be due to the dead and partly decomposed chloroplasts of the plankton Algae.

Layer I. From 0.5-2.0 cm. in thickness, this dark green or black layer is composed largely of organic de-

tritus, *i.e.* all kinds of plant and animal debris as described above. The material is semi-liquid in consistency, it abounds in bacteria and it contains very little mineral matter. Silt or sand grains falling to the bottom would settle right through this layer to rest on the next.

Layer II. From 2.5-4 cm. in thickness and composed of a thick, creamy, grey clay. This layer is predominantly mineral in constitution with a slight admixture of plant and animal detritus.

Layer III. This layer is 5 cm. in thickness and is made up of a stiffish grey clay as a matrix with black areas scattered through it. In some places this layer is almost completely blackened.* The detritus in this layer is limited to the cases of diatoms and Protozoa and coniferous pollen.

Layer IV. This layer extends at least 2 metres downwards from the lower limit of layer III. It is of stiffish, grey clay, similar to layer III, but lacking the black material. In sampling, a 12 lb. 1 1/4-in. pipe dropped a distance of 8 metres through the water was able to bury itself in this mud to a distance of 2 metres. Shells of diatoms and Protozoa are found scattered all through the clay.

As a measure of the organic material in these layers, determinations were made of the total organic nitrogen in three samples taken from each layer. These samples were taken at different parts of the lake at a depth of 30 metres. The averages of these results are included in the following tabular summary of the bottom layering.

This arrangement of strata was found to be almost uniform from depths of 25 to 45 metres, with slight variation in the thickness of the individual layers.

*Dr. E. M. Kindle of the Geological Survey, Ottawa, suggests that the black patches were due to a bacteriological action and cites a similar blackening found by himself in Bay of Fundy muds (1926). In the latter case, however, the black colour is thought to have appeared after the sample had stood for some time, while in Lake Simcoe deposits the black patches were present when the mud was first brought to view.

TABLE 6. Bottom layers in Lake Simcoe, at 30 metres depth.

Layer	Thickness	General characteristics	Percentage of moisture	Total organic nitrogen in p.p.m. on dry weight basis
A	0.05 cm.	A yellowish flocculent film not always present.		
I	0.2-2.0 cm.	Plant and animal detritus with little mineral matter.	89%	1.860
II	2.5-4.0 cm.	Thick, creamy green clay with little organic detritus.	84%	0.950
III	5.0 cm.	Stiffish grey clay and black patches, no true detritus.	76%	0.700
IV	2 metres	Stiffish grey clay uniform in composition.	74%	0.565

In these layers the microfauna was mostly confined to the upper half of layer I. When layer A was present the minute flagellates and ciliates were very abundant in it. The macrofauna were spread all through layer I; and some forms, especially the oligochaetes, were able to penetrate a short distance into layer II. The burrowing mayfly nymphs were never found more than 3 centimetres below the surface of the ooze. These nymphs are so active that it is difficult to say just where they were when the sample was taken. The chironomid larvae have their tubes in a horizontal position and are confined to layer I.

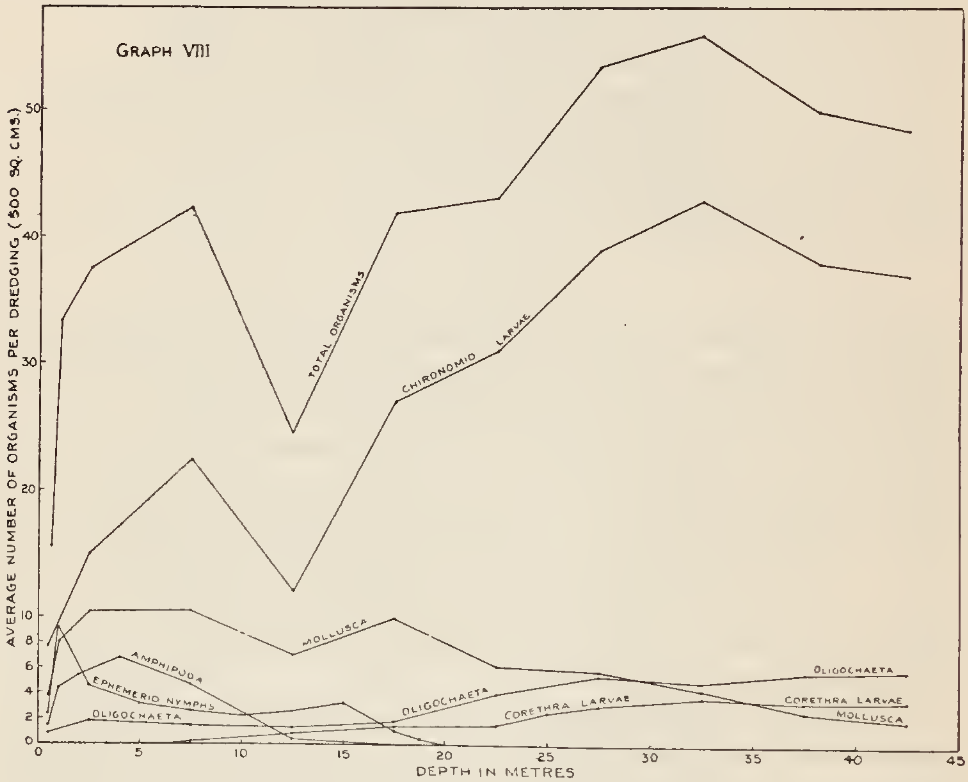
A further significance of the ooze layer and its inhabitants will be considered in Part II, dealing especially with the circulation of food materials and the transformations which they undergo on the bottom layer of the lake.

THE BOTTOM FAUNA AS A WHOLE

Having considered the distribution of the various groups of organisms separately, it is still necessary to assemble these data into a picture of the bottom fauna as a whole. Such a picture is not to be gained by studying the bathymetric distribution of bottom organisms alone. We must also take

into account their ecological distribution, including the position of one group relative to its neighbours.

Graph number VIII presents a composite view of the numbers and distribution of the six major groups of bottom organisms, *viz.*, chironomid larvae, Mollusca, Amphipoda, ephemerid nymphs, Oligochaeta, and *Corethra* larvae. The upper curve shows the distribution of the six groups com-



GRAPH VIII. Showing the relative numbers and distribution of the six major groups of bottom organisms as well as their total numbers and distribution.

bined. The omission of a number of relatively unimportant groups such as the Trichoptera and Hydracarina adds to the clarity of the graph. These groups combined make up only 6 per cent. of the total fauna numerically.

Certain features concerning the composition of the fauna as a whole are evident from an examination of the graph. The predominance of chironomid larvae is perhaps the most

striking feature. The comparative numbers of different groups could not be seen on the distribution graphs in the preceding pages since each curve was plotted to its own convenient scale. From shore to a depth of 15 metres the chironomid population is just less than the sum of all other forms. From 15 to 45 metres they greatly outnumber all other organisms combined and form 73 per cent. of the total population. It should be noted that the curves indicate numerical and not gravimetrical relations. The chironomid larvae form a smaller portion of the total fauna by weight than by numbers. The picture is even less representative of the relative values of different groups as fish food, for instance, the great bulk of chironomid larvae is less important as fish food than the seemingly insignificant numbers of ephemerid nymphs.

The bottom fauna, exclusive of chironomid larvae, is represented by the area between the curve of chironomid distribution and that of the total fauna. In the littoral and sublittoral zone this non-chironomid fauna is fairly large. In the deeper water, 15 to 45 metres, it maintains a fairly constant amount. While the total of this fauna is constant, the distribution of its separate components is quite irregular. In the shallow water the Gastropoda, Amphipoda and Ephemeroptera are predominant, while in the deeper water they are replaced by Pelecypoda, Oligochaeta and *Corethra*.

With reference to the distribution, rather than the composition, of the fauna as a whole, four distinct features are to be noted.

In the shore area, 0-1 metre, the population is represented as beginning at the small number of 15.5 per 500 square centimetres (the equivalent of one dredging). Shores are in general considered to have a rich fauna, this is, of course, disregarding the semi-barren and exposed shores. In Lake Simcoe the shore line is 44 per cent. exposed and stony, 33 per cent. bare sand with only 10 per cent. protected stone, 10 per cent. mud with aquatic vegetation and 3 per cent. sand with vegetation. The greatest numerical population anywhere in the lake is to be found in the protected stony bays and the

smallest population found on the wave-washed sand beaches. The shore area is therefore a region of extremes in population, but the predominance of exposed shore, 77 per cent., results in a low average population.

In following the distribution curve a large population may be observed between the depths of 3 and 8 metres where the littoral species are the most abundant and find most favourable conditions. As mentioned above, this peak is due largely to the Gastropoda, Amphipoda and ephemerid nymphs which characterize the littoral and sublittoral zones.

The number of organisms drops to a minimum at 12.5 metres. This feature is found in the distribution of most groups of bottom organisms in Lake Simcoe and it has been observed in several other lakes. Lundbeck (1925) explains the situation by saying that the sublittoral zone, in which the minimum occurs, is a region of transitional conditions between the littoral and the profundal zones. Since the sublittoral has little distinct fauna of its own, it is populated by a mixture of profundal and littoral species, neither of which find the conditions favourable.

A fourth point of special interest in the distribution of the fauna as a whole is to be found in the maximum abundance in the 30-35 metre zone. This peak is due to the chironomid larvae and does not correspond with the maximum fauna as measured by weight, the latter maximum being found between 20 and 25 metres, an important feature in view of the fact that bottom-feeding fish do most of their feeding at depths of less than 25 metres.

THE COMPOSITION OF THE BOTTOM FAUNA OF LAKE SIMCOE AS COMPARED WITH THAT OF OTHER LAKES

In dealing with the separate groups, comparisons have been made between the forms, number and distribution of bottom organisms in Lake Simcoe and those of other lakes. We may now compare the general constitution of bottom, fauna in different lakes. This subject is dealt with briefly since differences in the fauna of lakes will be discussed in later

sections under the factors limiting bottom fauna and the comparative productivity of lakes.

Lake Nipigon. The bottom fauna of Lake Nipigon differs most widely from that of Lake Simcoe in possessing large numbers of a deep water amphipod, *Pontoporeia hoyi.* The deep-water fauna of Lake Simcoe is largely composed composed of chironomid larvae. The difference is an important one since studies of fish food in the larger lakes have shown that amphipods are a staple food of bottom-feeding fish. A larger number of Oligochaeta is found in Lake Nipigon, but only at depths of more than 60 metres. Comparing similar depths in the two lakes it is found that the Oligochaeta in Lake Simcoe are slightly more numerous.

Lake Mendota. In Lake Mendota, Juday has demonstrated an enormous production of *Corethra* larvae in the deep water. In Lake Simcoe, *Corethra* larvae are relatively scarce. The whole fauna of the deep water in Lake Simcoe exhibits a greater variety than that of Mendota. This condition may be due to the greater stratification and resulting stagnation in the lower water of Lake Mendota since relatively few forms are able to withstand the greatly reduced oxygen supply. The shore faunas of the two lakes are quite similar in composition, but Lake Mendota has a greater quantity because it has a smaller percentage of semi-barren sand and stone shore.

Green lake. Juday (1924) studied Green lake, Wisconsin, a small, deep lake. The abundance of *Pontoporeia hoyi* and Oligochaeta in its deeper water suggests a resemblance to the fauna of Lake Nipigon and the Great Lakes, due no doubt to its great depth.

Oneida lake. The bottom fauna of a shallow bay in Oneida lake was studied by Baker (1916-18). The fauna was more than half composed of Mollusca. In even the richest molluscan habitat of Lake Simcoe (page 67) the population of this type was much smaller than that of Oneida lake.

North German lakes. Lundbeck's report (1925) of the investigation of 57 lakes in northern Germany shows a great variety of bottom fauna. Most of these lakes are small and

exhibit a much greater stratification than does Lake Simcoe. A larger one, the Plöner See, is in some features quite comparable to Lake Simcoe, as will be clearly indicated in a later section, page 94.

The Yxta Lakes, Sweden. Alm (1922) studied 19 Swedish lakes with special reference to the relation of bottom fauna to fish production. The fauna of these lakes resembles that of Lake Simcoe in having a predominance of chironomid larvae over all other organisms. Their fauna differs in having more *Corethra* and a smaller total quantity than that of Lake Simcoe.

FACTORS LIMITING THE QUALITY AND DISTRIBUTION OF BOTTOM FAUNA

The physical and chemical conditions that control the life and life processes in a lake may be unified by tracing them back to two fundamental conditions. The first is the shape of the lake, which must include its depth and area and the conformation of its shores. The second is the geographical position of the lake, including the nature of its drainage area and the climatic conditions of the region. These conditions are linked up with the fauna and flora of the lake to form a working unit or microcosm as Forbes (1925) so aptly expresses it.

Such conditions as the temperature and the chemical properties of the water are commonly spoken of as factors limiting the life of the lake. That they affect the life of the lake is not to be denied, but they are certainly not simple or isolated factors. The consideration of a few examples will serve to show that each of these "factors" is the culmination of a number of agencies.

The temperature of the water in a lake depends on its size and the climatic conditions which exist in the region. Thermal stratification, if it exists, is largely due to the depth and area of the lake, to the air temperature and to winds. The chemical nature of the water is directly affected by the dissolved and suspended materials washed in from the sur-

rounding country. It is also influenced by the temperature, the thermal stratification and by the life processes of its flora and fauna. Winds, acting upon a lake, according to its size and stratification, set up various currents and wave actions. These currents and waves have their effect on the temperature and on the deposition of bottom materials. Light is a limiting factor for plant growth and indirectly affects the distribution of animal life. Light penetration, on the other hand, is limited by the dissolved or suspended material in the water and by absorption into the water itself.

In this most complex manner are the physical and chemical factors of the lake interrelated and interdependent. In an equally complex manner the biological activities of the lake are interrelated both among themselves and with the physical and chemical activities. The "factors" must be separated for convenience in investigation and discussion but they should be thought of both as cause and effect and not as independent agencies.

The factors influencing the bottom fauna of Lake Simcoe are dealt with in the following order:

- Bottom deposits
- Water conditions
    - Temperature
    - Oxygen supply
    - Water movements (waves and currents)
    - Light penetration
- Biological conditions
    - Plants, protective, and food relations
    - Animal associations and competition
- Résumé of the most active factors in Lake Simcoe.

Bottom deposits

The character of the bottom affects the distribution of bottom organisms in several ways. The relation may be purely physical, as in the case of oligochaetes which are unable to penetrate hard clay. Certain chironomids are found in both mud and sand, but much more abundantly in the mud since food material is scarce on the sand bottom. The rela-

tion may have its effect through the respiration directly, as when silt clogs the respiratory mechanism or indirectly where an excessive decomposition of bottom materials reduces the oxygen supply to an amount insufficient for the needs of the organism.

The greatest variation in the character of the bottom is observed in the littoral zone where extremes from bare sand beach to rich muddy bays are found. The bottom materials of this zone contain a large proportion of inorganic matter as compared with the depositions in deeper water. In Lake Simcoe, stone, sand and mud are found at the water level ccording to the protection which the shore receives from wave action. In the lower littoral and sublittoral zones hard clay and marl are to be found as well as the three aforementioned types. In Lake Simcoe there is no definite shell zone (page 67).

The oozy bottom mud of the deep water showed little variation except in the thickness of its constituent layers (page 74). In Kempenfelt and Cook's bays the detritus was measurably deeper than in the open lake.

Throughout the lower littoral and sublittoral zones limitation of the fauna by the nature of the bottom is more noticeable than in the shore zone where the effect of wave action predominates over other factors. In the profundal zone the uniform character of the bottom makes it difficult to observe the effect of bottom deposits on the fauna.

A noteworthy example of limitation in distribution by the nature of bottom is furnished in Lake Simcoe by the larger pelecypods, *Lampsilis* and *Anodonta.* They show a distinct preference for soft sand bottom, being only occasionally found on mud or clay. In the deeper water, *Chironomus plumosus* is confined to the lower profundal zone with the exception of a few muddy areas in which it has been able to extend its upward range to a depth of 7 metres.

In Lake Simcoe the bottom fauna is varied to a comparatively small extent by the nature of the bottom, due to the magnitude of the deep-water area in which the bottom is of a uniform character.

The opposite extreme is found in Lake Vätter, investigated by Ekman (1922). Lake Vätter is a large lake, 90 by 15 miles, situated in southern Sweden. In the deep water of the lake were found five different kinds of bottom, each of which had a characteristic fauna.

Water conditions

Temperature. The direct limitation of the distribution of bottom organisms by temperature is not a frequent occurrence, although few of the deeper water inhabitants appear to be found there because of a preference for low temperatures. Lundbeck suggests that the glacial relict Crustacea are in this class of organisms preferring cold, deep water. *Pontoporeia* is not present in Lake Simcoe and *Mysis* is present in only negligible numbers, possibly due to a too warm summer temperature in the bottom water. A further direct effect of temperature has been described by Lundbeck with reference to the stimulation of seasonal migration among the bottom fauna. This movement is most striking in the case of chironomid larvae. The migration of *Chironomus plumosus* is indicated by a shifting of the maximum abundance over a depth range of 15 metres in one season. On account of the size of Lake Simcoe it was not possible in this study to make intensive observations in any one area, without which it is impossible to follow the course of migration.

In an indirect manner the temperature of the lake affects the food supply by limiting the plant growth. Mean temperature and the duration of the growing season both enter into this action. A more important indirect temperature effect is the influence on the gas content of the water due to thermal stratification.

Thermal stratification in Lake Simcoe is not as complete as that found in smaller lakes such as Lake Mendota. It is, however, more constant and much more effective than in Lake Nipigon. In the latter lake storms frequently destroyed the thermocline in the open waters (Clemens, 1923).

Although the data on the limnology of Lake Simcoe are

incomplete, table 1, page 14, shows in July a moderate stratification and a deficiency of oxygen in the deep water. This deficiency was beginning to appear on June 20 ($0_2=4.3$ p.p.m.) and had disappeared on August 30, when bottom oxygen determinations indicated 6.3 p.p.m. at 25 metres. It will be seen below that these determinations of bottom oxygen may not be fully indicative of the actual conditions under which the organisms are living.

Lake Simcoe apparently does not suffer from "winter stagnation." Observations taken on March 2, 1928, show a practically uniform temperature of 0.8°C. from top to bottom in 20 metres of water. The bottom water contained 9.45 p.p.m. of oxygen. Since an ice-layer 18 inches thick covered the surface of the lake, the surface water would have no means of renewing its oxygen supply. We may conclude that the life processes and the decomposition of bottom materials were so much reduced by the low temperature that the oxygen supply was not noticeably lowered.

The oxygen supply. The dissolved oxygen of the shallow water is usually quite sufficient for the needs of its fauna. Waves dashing on the shore cause a great aeration of the water, which has its effect on the shore fauna. A striking example of this is the occurrence of a stonefly nymph, *Perla* sp., on rocky shores of Lake Simcoe, although it is typically an inhabitant of the swifter, stony parts of streams.

The maintenance of an adequate supply of oxygen in the deeper water is a much more serious problem. The oxygen supply in the lower strata is dependent upon the circulation of water rather than on direct diffusion from the surface.

Metabolic activities of the bottom fauna and the decomposition of bottom debris combine to use up the oxygen of the bottom water. Since these processes go on in the upper layers of the mud there is a minimum quantity of oxygen in the mud, and a considerable gradient of increasing oxygen content may exist from the mud into the first two metres of water above it. Alsterberg (1922) demonstrated this condition and described it as "microschichtung" in contrast with the macroschichtung or greater stratification with which we

are familiar. As a result of this "microschichtung" the usual determination of bottom oxygen, made 1.5 to 2 metres above the bottom, may or may not represent the actual oxygen content at the surface of the mud. An oxygen content of 5 p.p.m. at 2 metres above the bottom may merely indicate a steep gradient from this value to an oxygen deficiency, *e.g.* 1.0 p.p.m., at the mud surface.

A few of the profundal species are able to withstand a complete deficiency of dissolved oxygen for some months. In Lake Mendota, during a three-month period of summer stagnation, there is frequently no free oxygen in the bottom water (Birge and Juday, 1911). Living under such conditions is found a fauna specially equipped for respiration under difficulties. The larvae of *Chironomus plumosus* have both ventral and anal blood gills and possess haemoglobin to aid in respiration. The Oligochaete, *Tubifex*, buries the anterior portion of its body in the mud but waves the posterior part in the water. A third inhabitant of stagnant-bottom types is the larva of *Corethra*, which is able to swim freely away from the bottom and come in contact with more highly oxygenated water.

In the deeper water of Lake Mendota, Juday found only four common forms, *Corethra punctipennis*, Oligochaeta, *Chironomus tentans* and *Pisidium idahoense* with a small number of *Protenthes choreus*. In north German lakes, Lundbeck found a similar paucity of species in the deep water. He believes that most of the bottom species are excluded from the deeper water by the lowered oxygen supply.

In Lake Simcoe a larger number of species, especially among the chironomids, occur in the profundal fauna. It is apparent that the lesser deficiency of oxygen in Lake Simcoe allows a greater number of species to penetrate the deep water, although the more abundant species are those with special respiratory adaptations and low oxygen requirements, *e.g.* *C. plumosus* and Oligochaeta.

In Lake Nipigon the instability of stratification and the magnitude of deep-water currents combine to ensure an adequate supply of bottom oxygen which rarely reaches a

value of less than 6 p.p.m. even at depths of 90 metres (Clemens, 1923). As a result it was found that the oxygen supply was not a limiting factor for the bottom fauna (Adamstone, 1924).

The carbon dioxide content of water is seldom sufficiently great to have any noticeable effect on the bottom fauna. In Lake Simcoe, with a moderate supply of bottom oxygen, the influence of carbon dioxide is considered negligible.

Water movements

Waves.—The effect of wave action on the shore fauna is one of the most obvious ecological relations in the lake. The waves act in two ways, by modifying the shore itself and by affecting the organisms which inhabit the shore zone. On the sand beaches the force of the waves causes frequent movement of the particles and the constant washing prevents the accumulation of nutritive organic debris. This type of shore in Lake Simcoe is the most sparsely populated region in the lake, supporting only a few chironomid larvae and nematodes. On the exposed rocky shores the food is less scanty and some bottom organisms find shelter between the stones and under their edges. These forms are all adpated to the strenuous conditions. Many, like the larvae of the beetle, *Psephenus*, have greatly compressed bodies, some are able to anchor themselves by sucking mechanisms, as the leeches, while others have reinforced bodies or cases to resist the wave action, such as the heavy-shelled molluscs or the mayfly nymph, *Baetisca obesa.* Muttkowski (1918) has made an extensive study of the shore fauna of Lake Mendota and presents full data as to the effect of wave action in limiting distribution. In Lake Mendota the effects of wave action were confined to the first metre of depth while in the larger lake, Simcoe, the direct effects were found to reach a depth of 2 metres. Indirectly, the effects of wave action extend to a much greater depth since they are instrumental in causing currents.

Currents.—The present knowledge of currents and their effects on the ecology of fresh water lakes is extremely limited. In larger lakes, such as Lake Nipigon or the Great Lakes, is

found evidence of currents in the rolling and dragging of gill nets. In smaller lakes the evidence is less obvious, but we must recognize the importance of currents in affecting such fundamental conditions as the bottom oxygen supply. Scott, in 1921, made an analysis of the physiography and geology of small inland lakes in Michigan. He discusses the origin and nature of currents in these lakes chiefly in connection with the processes of erosion and sedimentation. Lundbeck (1926) makes considerable use of currents in explaining the biological phenomena of small north German lakes. There is still a very great need for a thorough study of the nature of currents as applied to biological problems in inland lakes.

Sedimentation in lakes is directly affected by the existing currents. The inorganic materials such as silt are carried into the lake by streams or produced by wave action from the grinding of shore materials. The place where such material is deposited depends on the strength of the current and on the size and specific gravity of the particles. In a similar manner organic materials arising within the lake or swept in from the land are dependent upon currents for their distribution. The streams which drain into Lake Simcoe have not sufficiently strong currents to carry materials 8 to 10 miles to the centre of the lake. The continued deposition in the open water must be regarded as the result of currents which arise within the lake itself. Currents are known to be the agency responsible for the formation of "shell zones" in the sublittoral region of lakes. Lundbeck investigated these phenomena and found that the action of the currents included both the carrying and accumulation of empty shells and the transportation of living molluscs. The absence of a definite shell zone in Lake Simcoe is interpreted as the combined result of shore conformation and the irregular distribution of living molluscs rather than any lesser activity on the part of currents.

The stratification and aeration of the deeper water are dependent upon currents to a considerable extent. The transfer of oxygen by diffusion from surface to bottom is so

slow as to have little or no effect on the bottom water in the profundal zone. The amount of oxygen reaching this layer is dependent on the circulation of the water, including the spring and fall turnover and currents. These currents appear to be more or less active throughout all seasons with the possible exception of the winter period when the ice covers the surface and protects it from winds. The amount of oxygen present at the bottom is dependent on the rate at which decomposition and animal metabolism are using it up. This does not alter the primary statement that the currents control the amount of oxygen that reaches the bottom.

In contrast to these indirect methods in which currents affect the distribution of bottom organisms, we have instances in which the influence is direct in the transportation of living forms by currents. Lundbeck believes that Mollusca (*Pisidium*) are carried considerable distances by the current. His conclusions are based on observations of variation in seasonal distribution of these forms. They reached their maximum depth at the period of strongest currents regardless of other water conditions. The transport of bottom organisms in their immature stages must influence their final distribution. In some of the aquatic insects, *e.g. Chironomus*, *Corethra* or Ephemerida, the eggs are laid at the surface and the larvae live on the bottom in deep water. The immature stages may be carried great distances before reaching the bottom. *Corethra* larvae do not seek the bottom until they are of considerable size and are thus exposed to the activity of currents over a longer period than other insect larvae.

Light penetration. From observations made at different seasons it was found that Secchi's disc could be seen at an average depth of six metres in the water of Lake Simcoe. This comparatively high degree of transparency was further exemplified by the occurrence of phytoplankton at an unusual depth.

The daily vertical migration of Entomostraca and *Corethra* larvae observed in the lake is very likely a phototropic effect, but the movement has not been observed to have any effect on the general ecology of the lake.

Biological conditions

From the complex maze of biological interrelations we may discuss a few of the more important means by which the bottom organisms are influenced by the flora and fauna of the lake.

Plants. The rooted aquatic plants in the lake are limited by the bottom deposits, light penetration, water movements, temperature and the chemical condition of the water. These plants are important chiefly as shelter for the bottom organisms and to a lesser extent as food. The contribution which the dead, rooted aquatics make to the detritus is small in a lake of the size of Lake Simcoe.

The sheltering effect of the rooted aquatic plants is most readily observed in the littoral zone where these forms abound. Intensive studies of the "weed fauna" have been made by Richardson, Baker and Muttkowski. The effect of the rooted plants in the sublittoral is less easily observed. *Chara* beds in Lake Simcoe are found from 2 metres down to a depth of 15 metres and they are always thickly populated. The fauna of *Chara* beds is largely composed of the amphipod, *Hyalella knickerbockeri*, caddis larvae and gastropods. It was observed that the *Hyalella* and several species of caddis were found only in *Chara* at the deeper part of their range. *Chara* has the effect of sheltering and providing food for these forms, both directly and indirectly through the microorganisms which it harbours. It is also possible that at depths of 15 metres the amphipods and caddis benefit by the fact that growing plants absorb carbon dioxide and release oxygen. In the shallower water this effect is probably not felt since the oxygen is usually high (Klugh, 1926). In the same way, though to a lesser extent, the bottom covering of *Cladophora* supported a large bottom fauna. The occurrence of *Cladophora* at 13 and of *Chara* at 15 metres is evidence of the effective penetration of light into the water of Lake Simcoe.

The phytoplankton is limited by light penetration, temperature and the chemical nature of the water. In the living condition it has no effect on the bottom fauna, but the

dead phytoplankton adds to the bottom detritus and as such forms a major source of food for the bottom population.

The action of bacteria in causing decomposition of the organic constituents of the ooze is an important factor, especially in the deeper water. The effect of varying degrees and kinds of decomposition on the bottom fauna is probably great, although we as yet know very little about the process.

Animals. The effect of animals or animal communities on the bottom fauna is largely a matter of food. One bottom species preys upon another or competes with it for the same food. Most of the deep-water organisms are detritus eaters and the detritus includes a considerable quantity of microfauna. A smaller group of deep-water organisms preys on other members of the bottom fauna. Lundbeck has shown that some species of *Tanypus* and of *Cryptochironomus* eat smaller chironomid larvae and small Tubificidae. *Corethra* belongs to neither of the above groups, being a plankton feeder. Alsterberg (1924) and Lundbeck (1926) working independently came to the same conclusion, *i.e.* that *Corethra* distribution was limited by the numbers of its food organism *Cyclops.* As a result of observation in shallow water, Muttkowski suggests that *Corethra* eats detritus. It is quite conceivable that the feeding habits of a form which ranges over such widely different habitats should vary in these extremes of location.

In some few cases the competition for space may be a factor in the distribution of organisms, though the effect is usually active through feeding or respiratory activities. Parasitism among bottom forms is likewise unimportant.

The wider question of animal interrelations, especially that of the role of bottom fauna in the circulation of food in the lake, will be more fully discussed in Part II.

Résumé of the Principal Factors Active in Limiting the Distribution and Quality of Bottom Fauna in Lake Simcoe

The composition of bottom material assumes a moderate importance in controlling the distribution and quantity of bottom organisms in the littoral and sublittoral zones. In the

profundal zone the effect reaches a minimum because of the uniformity of bottom composition. Temperature, although it has important indirect results, appears to have little direct effect on distribution in Lake Simcoe since the chief "cold-stenothermic" organisms, relict Crustacea, are practically absent. The warmth of the bottom water is suggested as the excluding factor for these relicts. Thermal stratification and the resultant low oxygen supply in deep water is of more importance in Lake Simcoe than in a large lake such as Lake Nipigon. The lowered oxygen of deep water has a considerable effect in Lake Simcoe, but the resultant limitation of profundal species is less marked than in Lake Mendota or in Lundbeck's north German lakes. In a similar manner the currents are probably less active than in Lake Nipigon but have more effect in Lake Simcoe than they have in smaller lakes. Wave action is a powerful factor in Lake Simcoe because its shores are largely unprotected. The result is seen in the extreme paucity of organisms living on the bare sand and stone shores. The light penetrates deeply into the clear water of Lake Simcoe and results in a deep range of plant growth. The biological interrelations among the bottom organisms of Lake Simcoe are the usual complex combination of food competition and circulation.

LAKE TYPES

In the last decade European workers have accumulated data on the bottom fauna of a large number of lakes. As a result of these comparative studies they have made great progress in classifying lakes on a basis of variation in fauna and life conditions in the lakes.

Thienemann recognized distinct types of lakes characterized by differences in the species living in their profundal zones. For instance, a lake whose profundal zone was inhabited by the larvae of *Chironomus plumosus* differed in such fundamental properties as the oxygen content of deep water, from lakes inhabited by *Tanytarsus* larvae. In Thienemann's (1924) division the oxygen relations were the important factor.

Naumann (1921), comparing the plankton of lakes, distinguished, on a basis of the dissolved nutritive matter, two types, "Oligotrophic," poor in nutritive matter, and "Eutrophic," rich in nutritive materials. Since the oxygen in a lake is used up alike by living and dead organisms, it follows that an eutrophic lake is poor in oxygen, while an oligotrophic lake is rich in oxygen. Combining the classifications so far we have two types: I. Oligotrophic lakes, poor in food, rich in oxygen and with *Tanytarsus* larvae a typical profundal species; II. Eutrophic lakes, rich in food, poor in oxygen and with *C. plumosus* a typical profundal species. Thienemann distinguishes a third type, the "Dystrophic" lake, in which the humus content of the mud was more important in limiting the fauna than the oxygen or nutritive factors. This type was characterized by the larvae of *Corethra*.

After making a survey of the bottom fauna in 57 lakes in northern Germany, Lundbeck (1926) has made further divisions. His major contribution has been a division of each of the three main types, eutrophic, oligotrophic and dystrophic, into three subclasses according to the humus content of their bottom deposits. These three classes are: *A*, Oligohumus lakes, with thoroughly decomposed bottom; *B*, Mesohumus lakes with humus mud and slightly coloured water; *C*, Polyhumus lakes with humus or peaty mud bottom and humus coloured water. Lundbeck makes a classification of thirty possible lake types by a further division of mud classes, *A* and *B* on a basis of mud composition and a further division of trophic classes I and II on a basis of bottom fauna. Of these thirty possible types he has been able to find representatives of at least seventeen among the European lakes studied prior to 1926.

In the classification of Lake Simcoe we may disregard the meso- and polyhumus types which are small lakes with humus or peaty bottom. Humus bottom is the result of incomplete decomposition of allocthonous (shore or land produced) detritus, a condition which could only exist in small, somewhat stagnant lakes. The bottom of Lake Simcoe is, according to Lundbeck's classification, a definite

oligohumus type, that is, characterized by much-decomposed detritus. This material is also known to bottom investigators as "vollgyttja," in contrast to other bottom detritus known as chitingyttja, diatomeengyttja, etc., according as they show a predominance of the chitinous remains of Entomostraca, diatom cases, etc.

Lake Simcoe exhibits a lowered oxygen supply in the deep water and a moderately high production of plankton. It is therefore to be considered "eutrophic" rather than oligo- or dystrophic. That it is not entirely eutrophic is shown by the fact that its profundal fauna is not completely limited by the scarcity of oxygen (pages 84-85).

Having decided that Lake Simcoe is an eutrophic lake with an oligohumus type of bottom, we may compare the depth distribution of its fauna with that of other lakes of the same type. Diagram 2 is a copy of Lundbeck's diagram, illustrating the distribution by weight of bottom organisms in a typical eutrophic lake. On the left he has plotted the main factors limiting this distribution, and on the right we have added the distribution of bottom fauna by weight in Lake Simcoe. In Lundbeck's curves the littoral maximum is due to the combined effect of rooted aquatic plants *A*, the high oxygen content *B*, and the high temperature of the water *C*. The minimum in the lower sublittoral is due to the comparatively small numbers of sublittoral organisms. The profundal zone is marked by lowered temperature and oxygen, both of which fall off rapidly at the lower limit of the sublittoral zone since this coincides in a general manner with the thermocline. The maximum fauna in the upper profundal zone is followed by a decrease in the lower profundal. In the latter the mud deposits are much thicker and the oxygen content, which was small in the upper profundal, is still smaller in the deepest zone. The diagram presents a picture of theoretical distribution of bottom fauna in a typical eutrophic lake, but just such conditions were actually found by Lundbeck in the Plöner See.

The curve on the right represents the distribution by weight of bottom organisms in Lake Simcoe, plotted on the

same depth scale as the rest of the diagram. The two curves have in common three main features, a maximum in the shallow water, a minimum in the sublittoral and a second maximum in the profundal. In Lake Simcoe each of these points is found at a slightly greater depth than the corresponding point in the Plöner See. The reason for this shifting is obvious. In Lake Simcoe typical littoral conditions were found from 0 to 5 metres and sublittoral from 5 to 14, as compared with 0 to 4 and 4 to 12 metres in the corresponding zones of Lundbeck's lakes. Since littoral and sublittoral

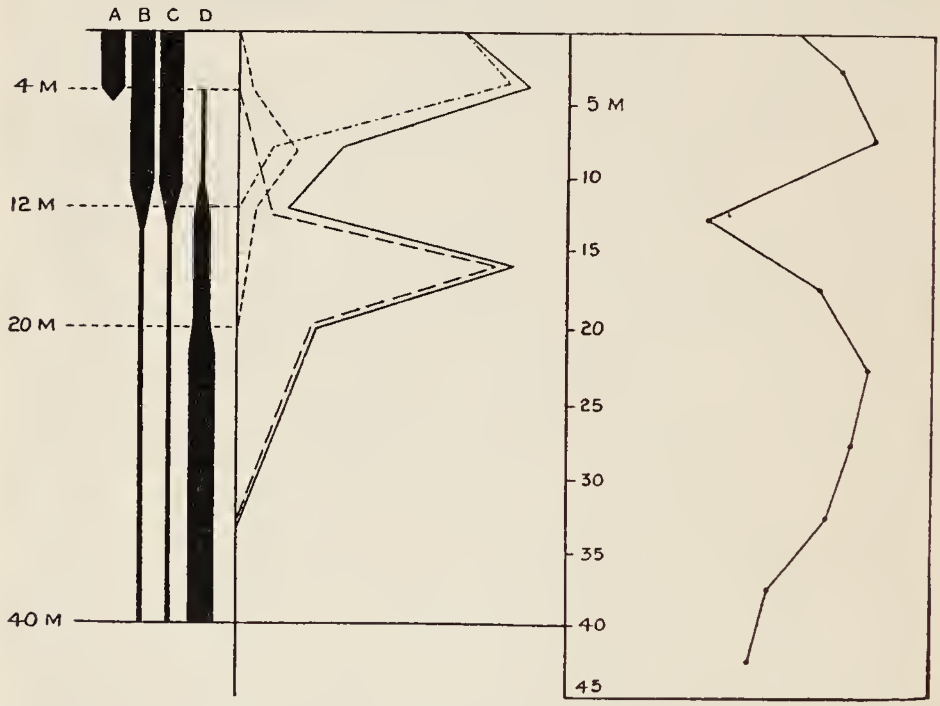


DIAGRAM 2. Curve showing the distribution of bottom fauna in a typical eutrophic lake (Plöner See). On the left is a diagrammatic representation of the limiting factors. On the right is the distribution of bottom fauna in Lake Simcoe.

Legend. Littoral fauna — - — - — - — Sublittoral fauna - - - - - -
Profundal fauna — — — — Total fauna ————
Rooted aquatic vegetation...A Oxygen content of water.....B
Temperature...............C Mud (detritus) deposits.....D

(Diagram after Lundbeck (1926) with the addition of the curve from Lake Simcoe)

conditions depend largely on wave action it is to be expected that the littoral and sublittoral zones will extend to a deeper level in a large lake than in a small one. Accordingly, the sublittoral minimum is found at successively greater depths in the distribution of fauna in the Plöner See, Lake Simcoe and Lake Nipigon.

A second difference in the distribution of fauna in Lake Simcoe is seen in the lower profundal where the production does not fall off as rapidly as it does at the corresponding depths of the Plöner See. This condition has already been referred to in connection with the oxygen supply. In the deep water of Lake Simcoe the oxygen is reduced but not to such a degree as to prevent the penetration of a number of species into the deep water. The lower profundal zone is, by reason of its greater oxygen supply, much more productive in Lake Simcoe than in the north German lakes.

The system of classification of lakes as presented by Lundbeck sums up the recent findings of European workers in this field. It accounts for the major differences in the bottom fauna of lakes on a sound basis of ecological conditions. The classification is unsatisfactory for large lakes such as Lake Nipigon, because in these lakes, due to the instability of stratification, the bottom fauna is not much affected by the factors which predominate in small lakes. That Lake Simcoe fits so well into the classification may be recognized as further evidence of the validity of the system.

B. THE QUANTITY OF BOTTOM FAUNA IN LAKE SIMCOE

The last section, which dealt with quality and distribution of bottom organisms in Lake Simcoe, was based largely upon the findings from 208 dredgings in the open water and 25 quantitative collections along the shore. The following section presents the quantitative analyses of the same dredgings, both from the numerical and gravimetrical points of view. The average dry weight of individual organisms has

been determined by experiment and is applied to convert the numerical data into gravitational form (page 25). In view of the seasonal variation in the amount of bottom fauna it should be stated that the 200 dredgings were spread fairly uniformly over the months May to October inclusive.

Table 7 shows the average number per square metre of the important groups of organisms found at different depths.

TABLE 7. Showing the average number of bottom organisms (of the major groups) per square metre, at different depths in Lake Simcoe.

Depth zone	Chironomid larvae	Ephemerid nymphs	Gastropoda*	Pelecyoda*	Amphipoda	Oligochaeta	*Corethra*	Trichoptera	Miscellaneous	Average No. of all organisms per sq. metre	Average dry weight of all organisms* in mgm. per sq. metre
Shore zone 0- 1m.	152	48	54	22	28	16	0	1	84	405	1028
0- 5m.	300	90	124	82	112	36	0	14	30	788	1280
5-10m.	450	54	130	78	138	30	2	10	34	926	1480
10-15m.	240	52	54	88	94	24	9	4	9	574	654
15-20m.	540	28	82	118	10	26	15	8	17	844	1170
20-25m.	620	0	9	114	2	80	30	0	92	947	1420
25-30m.	780	0	8	102	0	106	62	0	10	1068	1340
30-35m.	860	0	7	84	0	98	74	0	11	1134	1220
35-40m.	760	0	5	52	0	118	70	0	7	1012	950
40-45m.	740	0	6	34	0	120	72	0	6	978	852

*Weight of the mollusc shells deducted.

The above table serves to recall the relative abundance and distribution of the different groups of bottom organisms, although the same data have already appeared in graph VIII. The column of miscellaneous organisms includes nematodes, leeches, hydrachnids, the Odonata, and scattered representatives of other insect orders. The abundance of these forms near shore is indicated by an average of 84 per square metre in the 0-1 metre zone. It should be stated that the larger pelecypods are not included and that the weight of molluscs is given as body weight alone, exclusive of the shell.

Since the 5-metre depth zones are of unequal areas, page 11, an average of the dry weight of bottom fauna of the nine zones is not a true representation of the bottom fauna of the whole lake. Table 8 shows a further analysis of the data, including the dry weight of the total fauna supported in each zone.

TABLE 8. Showing the area, average amount of bottom organisms per unit area and total dry weight of organisms in each depth zone.

Depth zone	1 Dry weight of organisms in mgm. per sq. metre	2 in kilograms per hectare	3 Area of each zone in hectares	(2x3) Total dry weight of fauna in each zone in kilograms
0- 5m.	1,280	12.8	630,000	8,064,000
5-10m.	1,480	14.8	670,000	9,916,000
10-15m.	654	6.5	720,000	4,680,000
15-20m.	1,174	11.7	760,000	8,892,000
20-25m.	1,420	14.2	670,000	9,514,000
25-30m.	1,340	13.4	810,000	11,583,000
30-35m.	1,220	12.2	230,000	2,967,000
35-40m.	950	9.5	40,000	380,000
40-45m.	850	8.5	1,000	85,000
		Totals........	4,531,000	56,081,000

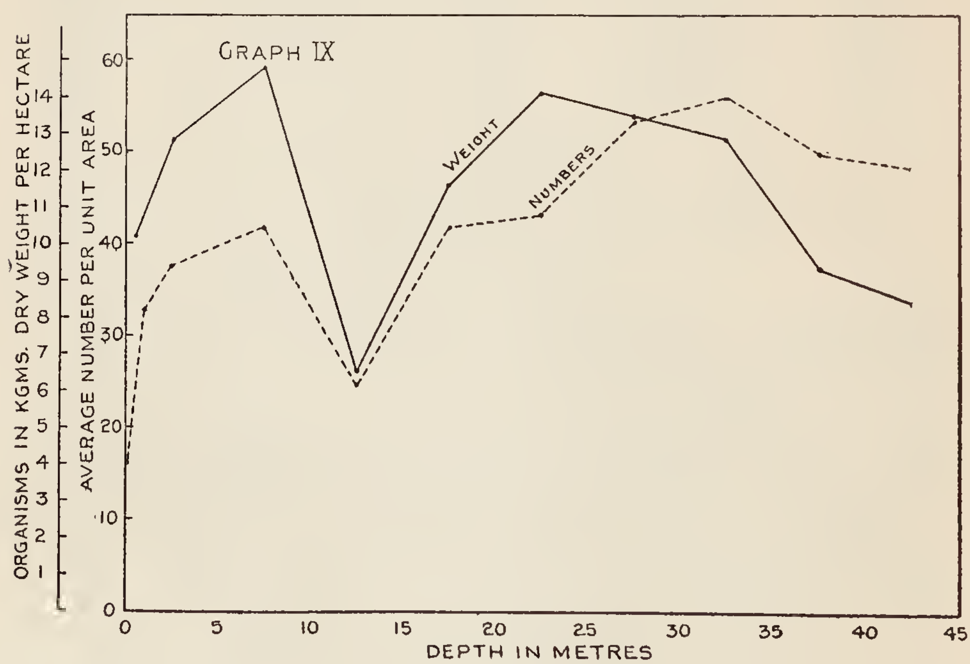
The total water area of Lake Simcoe is equal to 4,530,000 hectares and the dry weight of its total fauna is 56,081,000 kilograms. The average bottom fauna is therefore 56,081,000 $\div$4,530,000 = 12.38 kilograms per hectare or 11.0 lb. per acre (mollusc shell deducted).

It is probably more instructive to compare the bottom fauna in the ecological zones, littoral, sublittoral and profundal, than in the arbitrary depth zones used in tables 7 and 8. Table 9 shows the average number and quantity of bottom fauna in the various ecological zones of Lake Simcoe.

In table 9 two features are especially clear. The minimum fauna is found in the lower sublittoral, only 562 organisms per sq. metre, and a dry weight of only 6.3 lb. per

TABLE 9. Showing the amount of bottom organisms present in the various ecological zones of Lake Simcoe measured as numbers per square metre and kilograms dry weight per hectare.

Ecological zone		Average no. of organisms per sq. m.		Average dry wt. of organisms kgm. per ha.	
Littoral zone 0-5m.		788		12.8	
Sublittoral zone 5-14m.	Upper sublitt. 5-10m.	926	764	14.8	8.2
	Lower sublitt. 10-14m.	562		6.3	
Profundal zone 14-45m.	Upper prof. 14-24m.	868	1020	12.8	12.4
	Lower prof. 24-45m.	1097		11.7	



GRAPH IX. The distribution of all bottom organisms by weight ————, and by numbers - - - - - -

acre. In other words, the lower sublittoral zone supports only half the weight of fauna found in each of the other zones. In the profundal zone it is seen that the maximum number, 1097 per sq. metre, occurs in the lower profundal, while the maximum weight appears in the upper half of the profundal zone. The reason for this phenomenon was discussed on page 55, under chironomid larvae, since they are responsible for the position of these two maxima.

Graph IX has been constructed to show the difference between distribution of bottom fauna by weight and by number. In the curves on this graph the aforementioned maximum weight is in the upper profundal at 20.5 metres, and the maximum number is in the lower profundal at 32.5 metres. A further difference is to be seen in the littoral and sublittoral zones. In this region the weight curve rises highest from the numerical curve, indicating that in this region the organisms are heavier than in any other. On a further examination of the data it was found that this condition was due to the amphipods and larger gastropods which reach their maximum abundance in this region.

Summary

The quantity and composition of the bottom fauna of Lake Simcoe may be summed up as follows:

1. The average number of macroscopic bottom organisms over all depths is 820 per sq. metre, or 776 per sq. yard.
2. The average dry weight of all organisms over all depths is 12.38 kgm. per hectare, or 11.0 lb. per acre.
3. This fauna is composed as follows:

	By numbers	By weight
Chironomid larvae	61.5%	64.7%
Ephemerida	4.4%	5.8%
Gastropoda	5.3%	13.5%
Pelecypoda	8.6%	4.8%
Amphipoda	4.3%	2.2%
Oligochaeta	7.9%	2.7%
Corethra larvae	3.9%	1.4%
Trichoptera larvae	0.4%	0.4%
Miscellaneous	3.7%	4.5%

4. The distribution of the fauna is most clearly and concisely shown in graphs VIII and IX.

FACTORS AFFECTING THE QUANTITY OF BOTTOM FAUNA AND COMPARISON OF LAKE SIMCOE WITH OTHER LAKES

The quantity of bottom fauna is necessarily affected by the factors which we have described as limiting its quality and distribution. The division of the study into qualitative and quantitative aspects is convenient but quite arbitrary, since the quantity of the fauna depends to some extent on the quality, and the quality and distribution of the fauna are best studied by systematic quantitative sampling. Although the same factors are at work in each case, their effects may appear in a slightly different manner and a few additional factors may be involved.

The "type" of the lake and general factors

In the discussion of lake types (pages 91-95) it was seen that an "eutrophic" lake, of which Lake Simcoe is an example, had certain fundamental features. Eutrophic lakes have a rich plankton, a low oxygen content in deep water, definite thermal stratification, a well decomposed detritus bottom and a relatively large bottom fauna of a definite composition. That these features are definitely associated is suggestive of the fact that the amount of bottom fauna is affected by the type of bottom, temperature and thermal stratification, oxygen supply and the amount of plankton. Other factors mentioned as affecting the bottom fauna were the water movements, light penetration and biological associations, both plant and animal.

The richness of the lake

The total food in circulation, or the richness of a lake, is reflected in the amount of bottom fauna. This is to some extent limited by the amount of salts and organic matter supplied to the lake by its drainage basin. To a greater extent it is dependent on the nature of the lake itself, whether it is economic, as in an "eutrophic" lake where a large amount

of organic matter is in circulation, or whether it is inefficient, as in an oligotrophic and polyhumus lake, where large quantities of organic material are lost in its peaty bottom and the bottom fauna is scarce. It is probable that the "type" of the lake has more influence on the amount of its fauna than its situation in a rocky Archaean area or a rich sedimentary area, although it is recognized that the "type" itself is affected by the nature of the surrounding country.

The composition of the fauna

The composition of the fauna may have various effects on the total quantity of organisms. A given lake may not have in its fauna the most efficient organisms to turn its food into fauna. In another case the nature of the fauna may have been greatly modified by its geological history, as in Lake Nipigon, where the bottom fauna of the deep water is largely dependent on *Pontoporeia hoyi*, a glacial relict crustacean. The time factor is also to be considered as affecting the composition of the fauna. At any set time the fauna is at one stage in an evolution which includes the rising and falling of certain species or groups. Under such circumstances it is not to be expected that the total amount of fauna should remain constant. Observations by Lundbeck and Alm, page 116, on the yearly variation in the bottom fauna of certain lakes, indicate that these changes of the fauna may go on more rapidly than we should suspect any animal association to evolve.

Size (depth and area) of a lake

The depth and area of a lake affect the amount of fauna present. We have stated that depth has an effect on sedimentation, thermal stratification, currents, etc. Area, too, has its effect through these and other factors. In spite of the complexity of these interactions, a consideration of the relation between total fauna, depth and area of a lake brings out some significant results.

Observation shows that in general a lake of large area

supports a smaller population per unit area than a small lake. That this relation is due to certain physical differences need not interest us for the moment. In the same way it is observed that deep lakes usually support a smaller fauna than shallow lakes.

Green lake, Wisconsin, has an area of 12 sq. miles and supports an average fauna of 24 lb. per acre. Lake Mendota is 15 square miles in area and supports a fauna of 42.9 lb. per acre. Obviously these data do not support the above contention that large lakes are poorer in bottom fauna than small ones. The explanation of the situation is found in the depth of the two lakes, Lake Mendota having an average depth of 45 ft. in contrast to Green lake with an average depth of 109 ft. From this example it is clear that we must consider the two factors, depth and area together, if we would explain the amounts of fauna in lakes of different sizes.

It is less obvious, but quite definite, that there is a limit to the range over which increase in area continues to affect a decrease in amount of fauna. Lake Nipigon and Lake Ontario, for instance, have about one-half the amount of bottom organisms that Lake Simcoe has though they are many times its area.

We have suggested 40 square miles as a tentative limit at which area ceases to control the amount of bottom fauna. This does not mean that greater areas affect *no* decrease in fauna, but that areas greater than 40 square miles cease to have importance in this connection.

By a similar process it has been decided that depths greater than 100 ft. have no dominant effect on the bottom fauna.

Minimum as well as maximum limits of depth and area at which the bottom fauna is affected are no doubt existent. For instance, a lake or pond of two acres in area does not necessarily support a greater fauna than one of similar depth with an area of 10 acres. Such limits do not enter into the present discussion since none of the lakes under consideration are of such a magnitude.

The area, depth and amount of average bottom fauna in

seven lakes are included in table 10. Wherever possible, average depth is calculated with reference to the relative areas at each depth, *i.e.* average depth = volume ÷ area.

TABLE 10. Showing the size and amount of bottom organisms in seven lakes of eastern North America.

1	2 Investigator	3 Area in sq. mi.	4 Average depth in ft.	5 Maximum depth in ft.	(3x4) Area sq. mi. (up to 40) x average depth in ft. (up to 100 ft.)	6 Average bottom fauna in lb. dry weight per acre
Lake Mendota, Wisc.	Juday '22	15.2	44	84	669	45.10
Green lake, Wisc.	Juday '24	11.5	109	237	1150	24.0
Waskesiu lake, Sask.	Rawson	27.0	50	75	1350	13.7
Lake Simcoe, Ont.	Rawson	280	50	150	2000*	11.0
Lake George, N.Y.	Juday '22	74.4	80	187	3200*	7.6**
Lake Nipigon, Ont.	Adamstone '24	1750	180	410	4000*	5.23
†Lake Ontario	Adamstone '24	7050	300	738	4000*	4.3

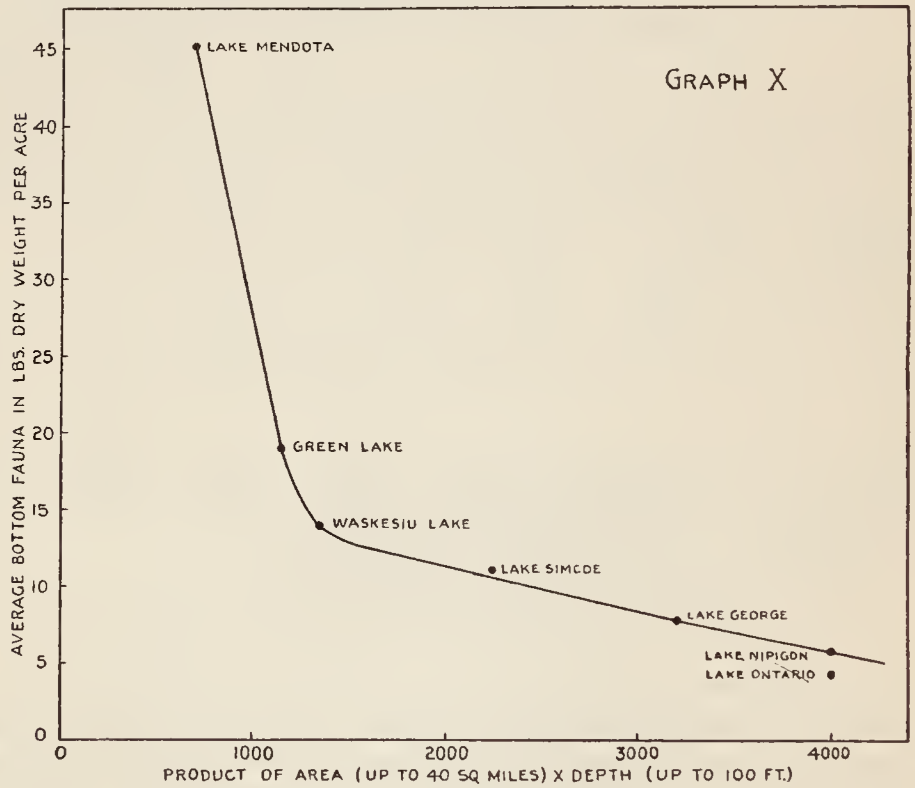
*Modified according to the limits explained below.
**Calculated from five dredgings in deep water.
†From a single series across Lake Ontario, Toronto to Niagara river.

Since the amount of fauna varies both with depth and with area, graph X has been constructed in which the average amount of bottom fauna in different lakes is plotted against the product of their separate depths and areas. Bottom fauna is expressed in pounds dry weight per acre, area in square miles and depth in feet. In cases where the area is greater than the limiting area (40 square miles) the depth is multiplied by the limiting area (*i.e.* by 40). Depth is treated in a similar manner.

From the curve in graph X it is evident that bottom

fauna varies with a definite relation to the product of depth and area. (The product of area × depth is not referred to as volume since the two factors should be thought of as distinct influences.) The relation between bottom fauna and depth × area as indicated by the curve cannot be represented by any single equation. Such a result is to be expected when the casual factors are so complex and the bottom fauna itself quite heterogeneous.

GRAPH X. The relation between the amounts of bottom fauna and the product of the depth and area (within limits) of lakes.



Graph X and table 10 include the estimates of the bottom fauna in seven American lakes on which extensive bottom surveys have been made. Two other lakes have not been included.

A thorough study of the bottom fauna of a part of Oneida lake was made by Baker, (1916, 1918). The average bottom

fauna was found to be 245 pounds per acre, a large quantity due chiefly to the large number of molluscs present. The estimate of 245 pounds was made by Richardson (1921) and refers to whole weight minus the shell, and not dry weight. Richardson's estimates both for Oneida lake and the Illinois river have been quoted along with dry weight estimates with a very misleading effect. Oneida lake is omitted from the graph and tables not because it fails to follow the depth-area relation, but because South bay, the area studied, was a shallow protected area and not representative of the lake as a whole.

The connecting lakes of the Illinois river, investigated by Richardson (1921, 1923) are not directly comparable to the above series of lakes. They are not strictly confined areas and they are subject to a very special influence in the flow of the Illinois river. The bottom fauna of these lakes is in the neighbourhood of 50 lb. dry weight per acre, exclusive of mollusc shell, while the Illinois river itself supports a bottom fauna of 98 lb. per acre.

The results of bottom fauna surveys in northern European lakes have always been expressed in live weight of organisms. Although we have some data on the relation of live weight to dry weight, we can at best make only a rough calculation of the equivalent value, since the percentage of moisture varies somewhat among the different organisms. Lundbeck's data on north German lakes, if transferred to a dry-weight basis, will be of special interest since the lakes are of dimensions for which the minimum limiting depth and area might be determined.

It is obvious that this relation is not universal. Certain lakes will deviate a great deal from the condition expressed by the curve. It is to be expected, however, that as the body of quantitative data on bottom fauna increase, it will be possible to define the curve and the upper and lower limits with increasing accuracy.

The relation between the quantity of the bottom fauna in a lake and the product of its depth and area may be expressed as follows:

"A small lake, less than one square mile in area, may be expected to support a large bottom fauna, more than 100 pounds dry weight per acre. In lakes of increasing size the amount of bottom fauna falls off rapidly until the product of the depth in feet and the area in square miles is approximately 1,300. A lake of this size supports an average bottom fauna of 10 to 15 lbs. dry weight per acre. From this point the bottom fauna decreases slowly until in the largest lakes it is in the neighbourhood of 5 lbs. dry weight per acre. In any lake depth over 100 feet and area over 40 square miles cease to affect the amount of fauna in any marked degree."

The meaning of this relation is that depth and area have such a fundamental effect on the secondary limiting factors, *e.g.* temperature, oxygen of the deep water, bottom deposits, etc., that the combined results of these secondary factors on the fauna can still be correlated with depth and area.

The chief factors which may result in a deviation from the above relation are the configuration of the shore line, the nature of the watershed and the climate of the country.

If a lake has a very irregular outline the effects of littoral conditions are spread over a large area. Aquatic plants and the mineral types of bottom occupy a larger proportion of the lake's area with considerable effect on the bottom fauna. In semi-enclosed bays the "protection" effect is so great that conditions are very much like those in a small lake. The relation of bottom fauna to depth and area is most applicable to lakes with moderate amounts of protected and exposed shoreline.

A lake in a rich, sedimentary country, surrounded by cultivated land, would be expected to support a greater bottom fauna than a lake of similar dimensions but situated in a rocky, Archaean type of country. Conditions such as these are represented by Lake Simcoe and Lake Nipigon. That Lake Simcoe supports a bottom fauna twice as great as that of Lake Nipigon may be partly due to this difference though too many other factors enter into the problem to allow a definite conclusion. Pearsall (1921) has called attention to the differences in the flora and fauna of lakes of different ages, *i.e.* primitive or evolved.

The fauna in different lakes of similar dimensions is affected by such climatic conditions as the temperature and exposure to winds. The temperature affects the rate of growth of bottom organisms and the length of the growing season, both of primary importance in the production of bottom fauna. Winds have their effect through the water movements which they produce, as explained on page 81.

In some cases the correlation between depth and area and amount of bottom fauna may appear to be lacking because of inaccuracy of the determination of the average bottom fauna. A single representative figure for the bottom fauna of a lake is by no means an easy determination. Granted that sufficient samples are taken, the result may still be influenced by variations in the experimental method, *e.g.* inclusion or exclusion of forms intermediate in size between macro- and microscopic groups, calculation of dry weight, inclusion of mollusc shells, etc. Another very important point to be dealt with in a later section is the variation in the quantity of bottom fauna present at different seasons.

The chief points of resemblance and difference between the bottom fauna of Lake Simcoe and that of other lakes have been brought into the above paragraphs. There remain some further comparisons, including discussion of the amounts of bottom fauna found on different types of shore.

The quantity of fauna in the shore zone, 0-1 m. deep, in Lake Simcoe

The numbers of various groups of organisms inhabiting this zone as a whole were included in table 9. In table 11 are found the number and dry weight of organisms on different kinds of shore together with the percentage of each shore type present around Lake Simcoe and the average shore production calculated with reference to these percentages.

In the shore zone of Lake Simcoe the bottom fauna varies from 1.04 kg/ha on bare sand to 26.1 kg/ha on protected stone shores. These are respectively the smallest and largest bottom populations to be found anywhere in the lake,

and they are found where we would expect to find them, in the region of most variable conditions. The predominance of exposed shores, 77 per cent. in Lake Simcoe, reduces the average quantity of bottom fauna in the shore zone to 10.28 kg/ha or 9.13 lb. per acre, which is slightly smaller than the average for the whole lake.

TABLE 11. The numbers and weight of bottom organisms on different types of shore (0-1m.), Lake Simcoe.

Type of shore	Percentage of each shore type in Lake Simcoe	Average No.* of organisms per sq. m.	Total dry weight of organisms in kgm. per hectare
1. Bare sand, exposed........	33%	43	1.04
2. Sand with vegetation......	3%	696	16.0
3. Bare stone, exposed.......	44%	227	5.96
4. Protected stone...........	10%	1468	26.1
5. Mud with vegetation......	10%	685	12.7
Average fauna over whole shoreline.................	405	10.28	

*Minute forms, *e.g.* Entomostraca, not included.

Adamstone (1924) emphasizes the barren nature of the shore in Lake Nipigon where "storms produce long stretches of barren rocky or sandy shore" and "where bottom organisms are few and aquatic vegetation is unable to gain a foothold."

In Green lake, Juday (1924) found the average shore fauna only 8.7 kg/ha, not much more than one-quarter the average for the whole lake. Richardson (1921) has estimated the fauna of the shore zone (0-1m.) of Lake Mendota at 67 kg/ha, which is probably a live weight since he compares it directly with the live weight of the fauna of lakes in north-eastern Illinois. If this is the case, the shore fauna of Lake Mendota, like that of Green lake, is poorer than the bottom fauna of its deeper water. The shore fauna of different lakes cannot be fairly compared in a direct manner, but rather on a basis of the amount of shore fauna relative to the total fauna. On this basis it is surprising that Lake Simcoe produces a

shore fauna almost equal to the average fauna in spite of the predominance of exposed shores.

Bottom Fauna of European Lakes

In order to make the available data on the bottom fauna of northern European lakes comparable with Lake Simcoe, the live weight measurements must be converted into dry weight. The examination of a large amount of data, chiefly from Juday (1922, 24), in which equivalent live and dry weights are given, reveals the fact that bottom organisms contain from 75 to 85 per cent. water, usually in the neighbourhood of 80 per cent. Using this value, results given in live weight may be converted into equivalent dry weights.

Table 12 shows the average bottom fauna of European lakes grouped and averaged.

TABLE 12. Comparing the bottom fauna of four groups of northern European lakes.

Lakes	Investigator	Average live weight of bottom fauna in kgm/ha	Calculated dry weight of bottom* fauna (20%) kgm/ha	Calculated dry weight of bottom fauna lb/acre
19 Swedish lakes......	Alm '22.....	34.7	6.9	6.1
10 Norwegian lakes....	Olstad '25...	59.2	11.8	10.5
18 Finnish lakes......	Järnefelt '25.	63.5	12.7	11.3
57 North German lakes	Lundbeck '26	798.5	159.7	142.0

*Averages from Lundbeck (1926).

In the above table it is to be noted that the values for the Swedish lakes refer only to the mud bottom. Also in Lundbeck's values for north German lakes the mollusc shells are included.

To make any satisfactory comparison with American lakes, the European lakes must be considered in somewhat more detail than that provided by the above table.

The Swedish lakes examined by Alm (1922) were small, from 5 acres to 2.15 sq. miles in area and mostly from 2.5 to 30

metres in depth. A résumé of the size and the bottom fauna yield of 12 lakes is given in table 13. The data are from Alm (1922, 23).

TABLE 13. Data on twelve Swedish lakes studied by Alm (1923).

Lake	Area in hectares	Area in sq. mi.	Maximum depth in metres	Average live weight of bottom fauna kgm/ha	Calculated dry weight of bottom fauna kgm/ha	Calculated dry weight of bottom fauna lb/acre
Landsjön.....	550	2.15	11	74.3	14.9	13.25
Väner........	557	2.17	89	6.6	1.3	1.15
6 small lakes..	100-400	0.39–1.5	26	13.9	2.8	2.49
4 very small lakes.......	2–62	0.08–0.2	9.1	85.0	17.0	15.0

Landsjön and Väner lakes are of similar area but the former lake supports a bottom fauna more than ten times that of Väner. The difference is partly a result of greater depth, the maximum for Landsjön being 11 metres and Väner having a depth of more than 89 metres. A further explanation is found in the fact that Väner is an oligotrophic lake, poor in plankton, with a high oxygen content, deep water and a varied but poor fauna, largely composed of relict amphipods.

Of the remaining ten lakes, the group of six with areas of 0.3 to 1.5 square miles, show an average bottom fauna of 2.49 lb. dry weight per acre. The group of four with areas of 0.08 to 0.2 square miles, have a greater fauna, averaging 15.0 lb. dry weight per acre. The difference in quantity of bottom fauna may be regarded as the same "area by depth" effect as that found among lakes in America (page 102).

The average bottom fauna of nineteen Swedish lakes investigated by Alm is remarkably small, both as compared with Lundbeck's figures for north German lakes and as compared with American lakes. Three different factors may be partly responsible for this condition. The group contains a large number of "low-producing" lakes, *i.e.* oligotrophic types with *Tanypus* or *Corethra* predominating in the fauna. In

general the lakes are situated in rocky rather than rich sedimentary drainage areas. The data include only the fauna from mud bottom and as such may not be quite representative of the whole lake.

The Norwegian lakes investigated by Olstad (1925) are less varied among themselves than those examined by Alm, so that the average of 63.5 kgm/ha live weight is fairly representative of all the lakes. The Scandinavian lakes are, on the whole, situated in a more rugged type of country than the German and Finnish lakes which have been studied. The difference in the amounts of bottom fauna may be in part the result of this factor.

Jarnefelt's investigation revealed a great variety in the bottom fauna of Finnish lakes. Six lakes produced less than 10 kgm/ha live weight, about 1.8 pounds per acre dry weight, eleven lakes supported an average fauna of 50 kgm/ha or 9 lb. per acre dry weight and in a single lake the bottom fauna was more than 300 kgm/ha or 53 lb. dry weight per acre.

For the north German lakes, Lundbeck gives an average quantity of 785 kgm/ha live weight. This may be made comparable with our results by deducting the weight of mollusc shell which leaves* 282.7 kgm/ha. Of this quantity the dry weight represents about 20 per cent., 56.5 kgm/ha or 51 lb. dry weight per acre. These lakes vary in area from 1.3 ha. (.05 sq. miles) to 3,130 ha. (12 sq. miles) and average 320 ha. (1.25 sq. miles). Their maximum depths range from 1 m. to 83 m., averaging 24 m. (79 ft.). On this basis the average lake, 1.25 sq. miles in area and with a maximum depth of 79 ft., produces a bottom fauna of 51 lb. dry weight per acre. The dispersion of the dimensions is too great to make this figure of any great significance. The Plöner See, one of the largest of the 57 lakes, and the one in which Lundbeck made the most intensive investigations, is much more comparable to Lake Simcoe and the results more instructive.

The Plöner See is 3,130 hectares in area or 12 sq. miles, and has a maximum depth of 60.5 metres. The two large

*Lundbeck's own estimate.

bays in which Lundbeck did most of his dredging have maximum depths of 31 and 44 metres. The average depth is not stated but from the data at hand it might be estimated as 25 or 30 metres for the whole lake. The bottom fauna for lakes of the type to which the Plöner See belongs amounts to 408 kgm/ha, of which 72 kgm. is chironomid larvae, 255 kgm. Mollusca and 81 kgm. other groups. Deducting the mollusc shell, which Lundbeck found to be 3/4 of the total body weight, the average bottom fauna becomes 217 kgm/ha, the equivalent of 32.55 kgm/ha dry weight or 29.3 lb. per acre. Using the data 12 sq. miles, depth 25 m. or 82 ft., bottom fauna 29.3 lb. per acre, we find that the Plöner See plotted on graph X comes very close to the curve midway between Lake Mendota and Green lake. It has not been recorded on the graph because it was necessary to estimate the average depth of the lake without conclusive evidence. The data are sufficient to show that the Plöner See supports a bottom fauna nearly equal in quantity to that of typical North American lakes of a similar size.

The Rate of Growth and the Annual Crop

The average amount of bottom fauna present throughout the summer season is not representative of the productivity of the bottom. A true estimate of the bottom productivity must take into account the rate of production as well as the amount of fauna present at a given time. The latter amount depends both on the rate of production and the rate of utilization or destruction. While these processes are, over a long period of time nearly equal, their rates vary at different seasons so that the fauna present at any given time is just a "balance on hand." Since the major fluctuations in the bottom fauna are seasonal, the annual crop is the most convenient measure of productivity although it is known that the crop varies somewhat in different years.

The annual crop of bottom fauna in a lake depends upon two factors.

1. The amount of fauna present at the beginning.
2. The rate of multiplication and growth.

From a fish food viewpoint it is seen that much of this crop is not available as fish food for the following reasons:

1. The fauna loses heavily by the emergence of certain adult insects.

2. Some of the fauna is in parts of the lake in which fish do not feed.

3. Some of the bottom fauna prey upon each other (reciprocal food relations).

Of the available food, the bottom-feeding fish cannot be expected to find and consume the whole amount. In view of these facts we see that only a small part of the annual increment in bottom fauna is utilized as fish food. It is quite clear, however, that the annual increment or crop is the best way of expressing the productivity or value of the bottom fauna, that is, if we are able to calculate this increment.

Although the observations on Lake Simcoe extended over a three-year period, the area was so great that it was impossible to repeat the examination of any one part of the lake in successive seasons. As a result we have no evidence of yearly fluctuation in the fauna of Lake Simcoe.

Various investigators have contributed to the study of the rate of growth of bottom organisms. Petersen (1911) suggested that the growth of marine bottom fauna was sufficient to double its quantity annually. The problem in fresh water is complicated by the inclusion of slow-growing species which live several years, insect larvae which live one or two years, and then emerge from the lake, and a third group which reproduces rapidly with more than one brood per season. Richardson (1921) reports observations on the rate of growth of a gastropod, *Vivapara contectoides*, in the Illinois river. He found an increase of 63 to 101 per cent. in the body weight, minus shell, over a twelve-month period. In the north German lakes Lundbeck found a yearly production of all mulluscs averaging 33 per cent. of the average summer fauna.

Lundbeck studied the annual production of chironomid larvae in the Plöner See and using data on the rate of growth, the numbers present, increase due to reproduction, decreases due to emergence and being eaten, he was able to determine

the annual crop to be 3 to 4 times the average summer fauna or 2 to 3 times the maximum number, *i.e.* the December fauna. With *Tubifex* the problem was less complex, and Lundbeck has placed the productivity at twice the total population, a figure which he applies to the rest of the fauna, *i.e.* exclusive of molluscs and chironomids.

The remaining groups are unimportant with the possible exception of the ephemerid nymphs and the Amphipoda. The latter have been found to produce several, as many as four, generations per year (Embody, 1912). In Lake Simcoe the amphipods are absent from the deep water and unimportant in the shallow areas. The ephemerid nymphs are not large in number, but relatively important as fish food. It is known that some of the Ephemeridae spend at least two years in the nymphal state (Morgan, 1913).

Seasonal Variation in Amount of Bottom Fauna

The most comprehensive investigation of seasonal variation in bottom fauna has been carried out by Lundbeck, chiefly on the Plöner See. From monthly observations over a period of two years he was able to follow the fluctuations in the number, size and total weight of chironomid larvae. His results have been discussed in some detail on page 57, and comparisons made between the chironomids of the Plöner See and the chironomid fauna of Lake Simcoe. He was able to follow the whole life history of the two more abundant species of *Chironomus*, *C. plumosus* and *C. libeli bathyphilus*, including their period of emergence, the rate of growth, the periods of maximum and minimum occurrence and the decrease in numbers due to mortality, *e.g.* being eaten by fish. Combining this with similar data on *Corethra*, Oligochaeta and *Pisidium*, he was able to show and explain the seasonal variation of total fauna. Since the fauna of the Plöner See, like that of Lake Simcoe, is composed largely of chironomid larvae, the variation in total fauna followed the variation in chironomid larvae, *i.e.* a minimum in July with the maximum emergence of adults, rapid growth of the new generation to a

aximum in December, a decrease due to mortality in the spring and the minimum again with that year's emergence. The magnitude of this seasonal variation in total bottom fauna, and in chironomid larvae since the two quantities vary in unison, is seen in the fact that the minimum fauna, in July, was one quarter as great as the maximum in December.

In Lake Simcoe the best illustration of seasonal variation is found in the *Corethra* larvae. The numbers of *Corethra* larvae in the profundal zone vary from 38 per square metre in May to a definite minimum of 9 per square metre in late July, an increase to 42 per square metre in October and 70 per square metre in early November. The minimum in July is obviously the period of greatest emergence. That the maximum number of the new generation was not found until November is evidence in support of Juday's (1922) observation that the immature larvae are at first free-swimming and seek the bottom after attaining a considerable size.

The small numbers of *Corethra* larvae render them quite insignificant in affecting the variation of the total population in deep water. Chironomid larvae are the large part of the fauna in Lake Simcoe, but unlike the chironomids of the Plöner See those of Lake Simcoe show no distinct summer minimum. This situation has been explained as due to the variety of species present in the deep water with a corresponding variety of periods of emergence. The overlapping of these periods of emergence prevents the appearance of any distinct minimum and as a result it is probable that the total fauna shows less variation than that in the Plöner See. Since the examination of the fauna in Lake Simcoe extended from May to October, inclusive, the average determination does not include the winter maximum of fauna, it does, however, include most of the season of active growth, so that it probably approximates the average yearly fauna.

Annual Variation in Amount of Bottom Fauna

That the quantity of bottom fauna might vary slightly over a period of years is quite conceivable. That it should

vary greatly from one year to another is difficult to understand, yet such a condition has been clearly demonstrated. Lundbeck (1926, p. 262) shows that the total weight of fauna in a bay of the Plöner See was, in the growth season 1924-25, almost twice as great as the total for 1923-24. Alm (1922), working on Swedish lakes, had demonstrated a decrease of similar proportions between the total quantity of fauna of the season 1918-19 and that of 1919-20.

Changes of a lesser magnitude might be explained on a basis of the ecological succession within the lake or as a result of the periodic fluctuations. An increase of nearly 75 to 100 per cent. in the amount of fauna present in successive years is yet to be explained and suggests a fruitful field for investigation.

Annual Production of Bottom Fauna in Lake Simcoe

Using Lundbeck's determinations of yearly productivity, *i.e.* three times the summer average for chironomid larvae, one-third for molluscs and twice for the remainder, we may calculate the annual production of bottom fauna in Lake Simcoe as follows:

Organism	Average amount fauna May-October kgm/ha	Rate of productivity (after Lundbeck)	Annual production kgm/ha
Chironomida larvae	8.06	x3	24.18
Mollusca	2.22	x1/3	0.74
Remaining fauna	2.10	x2	4.20
		Total	29.12

At this rate of productivity, Lake Simcoe, with an average summer fauna of 12.38 kgm. per hectare, would have an annual production of 29.12 kgm. per hectare or 25.87 lb. per acre. The fact that the composition of the fauna of the Plöner See resembles that of Lake Simcoe might suggest that Lundbeck's rating is not altogether inapplicable, although it

is recognized that the lakes of northern Germany have a somewhat longer growing season than Lake Simcoe.

RÉSUMÉ OF THE GEOGRAPHICAL AND LIMNOLOGICAL FEATURES OF LAKE SIMCOE

Lake Simcoe is a part of the Trent valley system of waterways and drains into Georgian bay through the Severn river. It is situated about 40 miles north of Toronto in a drainage area of 1,100 sq. miles, most of which is cultivated land; some, however, is swampy and wooded.

The area of the lake is 280 sq. miles, its average depth 17 metres (54 feet) and its maximum depth 44 metres. With the exception of two long bays, the lake is an open expanse of water about 15 miles in diameter, the shores being mostly exposed and of a sandy or rocky nature.

The water is somewhat alkaline, pH 8.1, cool and fairly well oxygenated. At midsummer a moderate stratification occurs and the bottom water has an oxygen content as low as 2.0 p.p.m. The temperature of the bottom water at this time is about 10°C. at the average depth, 17m. As a result of a fairly high transparency, the light penetration is somewhat deeper than in most lakes of similar size.

SUMMARY OF PART I

The Bottom Fauna

(*a*) *Composition and Distribution*

The bottom fauna is largely composed of six major groups which are considered in order of their numerical abundance, as follows:

Chironomid larvae belonging to at least 8 species and subgenera, make up more than 60 per cent. of the total fauna, *Chironomus plumosus* being the largest and most abundant species. The chironomid larvae are abundant at all depths, but show a minimum number in the lower sublittoral zone

(12m.) and a maximum abundance in the profundal zone (14-45m.).

The **Mollusca** taken include 40 species of gastropods and 15 of pelecypods, the latter group being slightly more numerous as to individuals but less varied as to species than the former. The Gastropoda are mostly confined to the upper 20 metres while the Sphaeriidae are most numerous at 20 metres and decrease gradually in shallower or deeper water. The molluscs constitute 13.9 per cent. of the total bottom population.

The **Oligochaeta** (Tubificidae) make up about 8 per cent. of the total fauna numerically. They are present at all depths but most constant and abundant in the deeper water (25-45 m.).

The **Amphipoda** of Lake Simcoe are practically confined to the littoral and sublittoral zones (0-14m.) and they are accordingly much less important than the amphipods of lakes in which the deeper living forms (*Pontoporeia*) are found.

The burrowing **ephemerid nymphs** are numerous in the sublittoral zone of Lake Simcoe. All the mayfly nymphs (Ephemeroptera) are confined to the upper 20 metres.

Corethra larvae make up a small proportion of the bottom fauna of Lake Simcoe. They are most numerous in the lower profundal zone (25-45m.).

The distribution of the chironomid fauna has been indicated above. The non-chironomid fauna is fairly constant in numbers in all depths. In the littoral and sublittoral zones this non-chironomid fauna is largely composed of Gastropoda' Ephemeridae and Amphipoda, while in the deeper water these forms are practically absent and the fauna is made up of Oligochaeta, Sphaeriidae (*Pisidium*) and *Corethra* larvae.

(*b*) *The Quantity of Bottom Fauna*

The average number of macroscopic organisms over all depths is 820 per sq. metre (776 per sq. yard). The average dry weight of macroscopic organisms over all depths is 12.38 kgm per hectare (11.0 lb. per acre). The greatest number of organisms (1,097 per sq. metre) is found in the lower profundal zone (20-25m.) and the greatest dry weight (14.8 kgm.

per hectare) in the upper sublittoral (5-10m.) The least number (562 per sq. metre) and the least weight (6.3 kgm. per hectare) are found in the lower sublittoral zone (10-14m.). A summary of the total quantity of bottom fauna and its composition is found on page 99.

(c) *Factors in the Ecology of the Bottom Fauna*

The factors affecting the distribution and constitution of the bottom fauna which have been considered, include bottom deposits, water conditions such as temperature, oxygen content, waves, currents and light penetration and biological conditions such as the protective, nutritive or competitive relations with other animals and with plants. A résumé of the principal factors affecting the fauna of Lake Simcoe appears on page 90. It has been demonstrated that the non-biological factors are inter-dependent and that they can be traced back to two fundamental conditions, the size of the lake, including its depth, area and shore conformation, and its geographical position, including the nature of its drainage area and the climatic conditions of the region.

Lake Simcoe has a fairly rich plankton and bottom fauna, a low supply of oxygen in the deep water and a thoroughly decomposed bottom ooze. In the classification of lake types developed by Naumann, Thienemann, Lundbeck and others, these life conditions would indicate that Lake Simcoe is an eutrophic type with oligohumus bottom deposits. That the distribution and quantity of bottom fauna support this conclusion is shown by the comparison between Lundbeck's theoretical distribution of fauna in an eutrophic lake and the actual distribution in Lake Simcoe, diagram 2, page 94. Lake Simcoe differs slightly from the typical eutrophic lake in having a lesser deficiency of bottom oxygen in the deeper water, which results in a larger number of species and a greater total fauna in its profundal zone than in that of other eutrophic lakes.

The minimum number and quantity of several groups of organisms were found to be in the lower sublittoral zone

(10-14m.) as was the minimum for the total fauna. Lundbeck suggests that the life conditions in the sublittoral zone are transitional between those of the littoral and profundal zones. Since the sublittoral zone has little fauna distinctly its own, it is populated largely by stray littoral and profundal species, neither of which thrive in the sublittoral conditions. The three main features which mark the distribution of fauna in eutrophic lakes, *viz.*, a maximum in shallow water, a sublittoral minimum, and a second maximum in deep water, were each found at slightly lower depths in Lake Simcoe than in Lundbeck's north German lakes. This appears to be the result of Lake Simcoe's greater size and exposure and the corresponding deeper effects of wave action and other surface conditions. In Lake Nipigon the sublittoral minimum was present at a level still lower than that in Lake Simcoe, which might be expected in a still larger lake subject to more active water movement.

The factors affecting the quantity of bottom fauna are necessarily the same as those which affect its quality and distribution, but they may be considered from another point of view. It has been demonstrated that the depth and area exert such a fundamental effect on the "factors" limiting the bottom fauna that the quantity of bottom fauna may be correlated directly with the depth and area, graph X, page 104. These two factors cannot be correlated separately with the amount of bottom fauna but their product shows a definite relation to the latter quantity. Certain factors, chiefly irregularity of the shore line, may cause a deviation from this relation.

A consideration of the seasonal variation and rate of growth of bottom organisms has resulted in an estimated annual crop or production of 29 kgm. dry weight per hectare (25.8 lb. per acre) over all depths in Lake Simcoe, as compared with the average standing amount of 13.8 kgm. per hectare (11.0 lb. per acre).

PART II

THE ECOLOGICAL RELATIONS OF THE BOTTOM FAUNA IN A LAKE

THE CIRCULATION OF FOOD MATERIALS IN A LAKE

Our conception of the amount of living matter and potential food-forming material in a body of water as large as Lake Simcoe is likely to be somewhat inadequate. Besides the myriads of living plants and animals there are the dead organic matter and the nutritive inorganic materials which have been accumulating in the lake for the last 20,000 years.* In comparison with this great "capital" the amounts of organic or nutritive inorganic materials added in any single season from the drainage basin, or the amount swept away at the outlet of the lake can be ignored while we discuss the transformations which proceed within the lake itself.

In the water, as on land, the principle of food chains and the nitrogen cycle have long been recognized. The photosynthetic activity of the phytoplankton providing food for microscopic animals and these minute animals providing food for the larger members of the fauna has been a matter of common knowledge and frequent reference. In spite of this knowledge few realize the complexity of the whole system and there are certain features of the circulation which have received very little attention.

Diagram 3 is an attempt to organize the available knowledge of the circulation of food materials into a single comprehensive picture. The scheme is chiefly applicable to the open waters of the lake since in the shore area additional factors render the relationship even more complex.

Nutritive matter occurs in the lake in five conveniently separated states, represented by the contents of the five circles on the diagram. They are: 1. The inorganic nutritive materials dissolved in the water. 2. The plankton, the higher aquatic plants and the microfauna which is sheltered

*Estimated age of Lake Simcoe from data given by Coleman (1922).

by these plants. 3. The fish fauna. 4. The bottom fauna. 5. The organic detritus of the bottom deposits.

The lines connecting the circles represent processes by which food materials are transformed, *i.e.* the paths by which nutritive materials circulate in the lake.

Path **a** represents the fundamental process of photosynthesis, the only means by which inorganic materials can be elaborated into organic or living substance and thereby be made available as food for the animals of the lake.

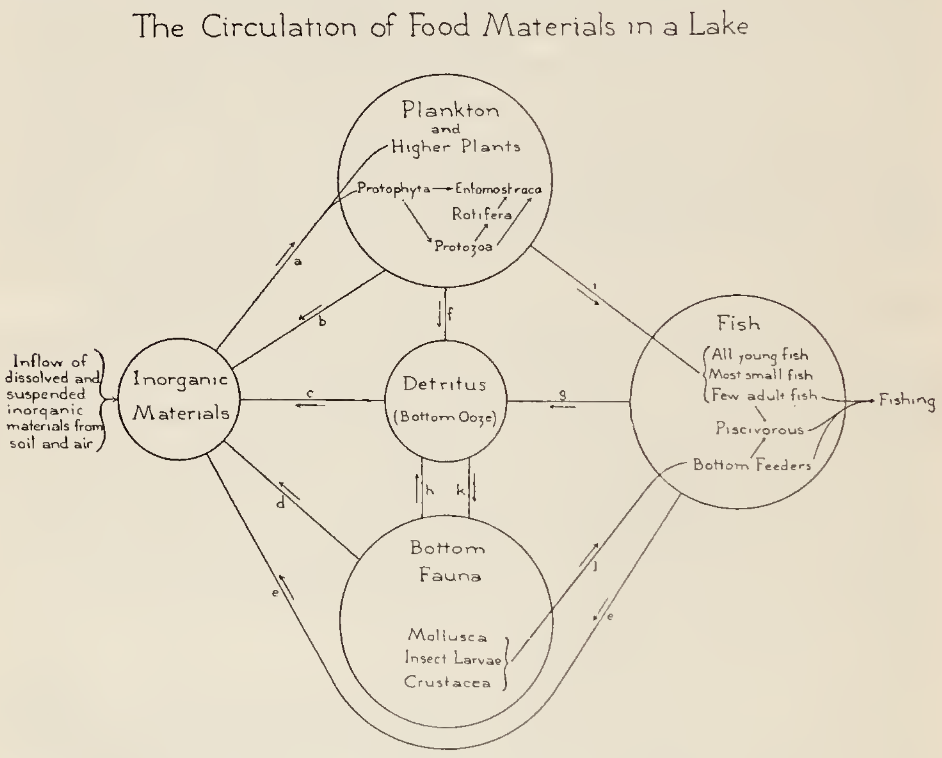


DIAGRAM 3. The circulation of food materials in a lake.

Paths **b**, **c**, **d** and **e** represent the processes of decomposition, largely due to bacterial activity which result in the destruction of organic matter. Decomposition does not always result in the immediate production of inorganic materials. It is known that large quantities of dissolved and colloidal organic matter are present in the water at all times. Since this material is rarely if ever utilized by living organisms

without being further broken down into inorganic salts it is not necessary to represent the dissolved organic materials in our scheme of circulation.

Paths **f**, **g** and **h** indicate incomplete disintegration and settling of plant and animal materials to form the organic detritus of the lake bottom.

The remaining paths, **i** and **j**, represent the feeding of fish on the plankton and on the bottom fauna, while path **k** indicates that the bottom fauna is made up for the most part of detritus eaters. The processes represented by paths **a**, **c**, **f**, **i**, **j**, and **k** are so well recognized as to need no further comment. The remaining five are admittedly less important but still worthy of consideration. Of these, **b** calls our attention to the fact that some of the decomposition products of dead plankton may be dissolved out before the remains settle to the detritus layer; **d** indicates that some of the bottom fauna, *e.g.* larger pelecypods and gastropods, on decomposing, are not scattered as detritus but dissolved as they decompose; **e** and **g** represent the decomposition of fish which die in the lake. Just how many fish come to this fate cannot be estimated but it is thought that the number of fish caught is much less than the number which reach maturity, and we know that some of the most abundant fishes of the lake (ling, perch and sucker) are rarely caught. From this evidence it would seem that the quantity of fish dying in the lake is not to be disregarded. Path **h** represents the fate of the bottom organisms which fail to be eaten by fish or by other bottom organisms.

The arrow on the left indicates the inflow of nutritive materials from soil and air. Especially important in this connection are such nutritive salts as the nitrates and phosphates. The chart does not mention the organic material which is washed in to add to the detritus since in a large lake the amounts of such allocthonous detritus is negligible. On the right a second arrow represents the loss of organic material from the circulation through the agency of fishing. In a simple chart it is not possible to represent other losses, due to emerging adult insects, or the outflow of water. In each case

there appears to be some compensation for the loss, *e.g.* many of the insects drop back into the lake and for everything swept out at the outlet of the lake a similar or greater amount is washed in by the inflow of streams. The outflow of a lake is therefore not to be thought of as a leak in the circulation system, and in a large lake the outflow is not sufficiently rapid to produce marked effects even on the life near the outlet. A calculation has indicated that at the average rate of outflow from Lake Simcoe it would take roughly 22 years for the present volume of water to pass through the Narrows at Atherley.

The circulation of nutritive material or food relationships as indicated in the chart is not a simple cycle but a combination of a number of cycles. For convenience we may represent the five states of food as *I*, *P*, *F*, *B*, *D*, denoting: Inorganic materials, Plankton, Fish, Bottom fauna, and Detritus, respectively. The cycles represented by $I \rightleftarrows P$ and $I \longrightarrow P \longrightarrow D \longrightarrow I$ represent the growth and destruction of plankton organisms without any utilization either by bottom fauna or by fish. Similarly, $I \longrightarrow P \longrightarrow B \longrightarrow D \longrightarrow I$ and $B \rightleftarrows D$, represent cycles involving the production of bottom organisms but still no fish. It is thus possible to have a large amount of life and a great food circulation with little utilization by fish. In a similar manner the possibility of five more cycles involving the utilization of either plankton or bottom organisms by fish can be demonstrated.

The diagram is limited in being applicable chiefly to the open water. In the shore areas other factors, chiefly the higher aquatic plants, cause a further complication of the scheme. It also fails to show the relative importance of the different processes, a defect which might be remedied by making the lines (paths) of different intensities, but at the risk of adding to its complexity. The purpose of the scheme, however, is to show the intricate nature of the circulation and something of the processes through which it is accomplished. In addition it demonstrates the unity of the whole process, a view well expressed by Dr. Forbes (1887) in his "Lake as a Microcosm."

THE FOOD OF FISHES IN LAKE SIMCOE

In the general nutritive system of the lake the question of fish food is of more than ordinary interest, especially from an economic point of view. Since this investigation was centred about the bottom fauna, the food of bottom-feeding fish received more attention than that of the piscivorous or of the plankton feeders. The following conclusions as to the food of various fish are based upon an examination of the stomach contents of 214 fish. Unless otherwise stated, the specimens were taken during the period between May 1 and October 30. This distribution of the observations is necessary since the food taken by fish at a particular season may not represent its usual diet. It is also noted that the fish were of average adult size, the food of young fish being examined only in exceptional cases.

THE WHITEFISH (*Coregonus clupeaformis*)

The stomach contents of 42 whitefish of average size (1 lb. 2 oz.) taken from eight different parts of the lake between May 1 and October 30, were made up of the following organisms:

Molluscs (chiefly *Pisidium*) occurred in 37 stomachs in an average quantity of 28%.

Ephemeridae—large nymphs occurred in 27 stomachs in an average quantity of 35%.

Chironomid larvae occurred in 18 stomachs in an average quantity of 14%.

The molluscs eaten by the whitefish were largely composed of *Pisidium* with small numbers of *Amnicola*, *Valvata*, *Planorbis*, *Physa* and young *Campeloma*. Although the average quantity of Mollusca per stomach was smaller than that of the ephemerid nymphs, the molluscan part of the food was more constant, occurring in a larger number of the stomachs examined. The ephemerid nymphs varied at different seasons from a mere trace to 95 per cent. of the contents of individual stomachs. They were the large burrowing forms, mostly *Hexagenia* with some *Ephemera*. Three less important food organisms, Ostracoda, Hydracarina and

Amphipoda, were found in the stomachs. The ostracods were often numerous but they are so minute that their nutritive value is negligible. Hydrachnids were unusually plentiful, occurring in 18 of the stomachs and averaging 6 per cent. of the total contents. Small quantities of *Chara* and *Cladophora* were found in several stomachs, but they are thought to have been taken by accident while the fish were feeding on the bottom organisms for which these plants provide a shelter.

Seven whitefish caught by angling at Jackson's point on November 7, 1928, were found to have eaten ephemerid nymphs 80%, chironomid larvae 10%, caddis and other insects 5%, *Pisidium* and *Amnicola* 5%. These specimens were taken in 10 metres of water and indicate the abundance and the utilization of mayfly nymphs at such depths. Although spawning had just begun, most of the fish appeared to be feeding freely.

The stomachs from whitefish taken at Beaverton on February 15, 1927, contained a number of lake shiners, *Notropis atherinoides*, and sticklebacks, *Eucalia inconstans*. While most of the former were undoubtedly those supplied as bait by the fishermen, it is improbable that the sticklebacks were from this source. The remainder of the contents were composed of ephemerid nymphs, chironomid larvae with a few caddis larvae and *Pisidium*.

A lot of 12 stomachs from whitefish caught at Jackson's point, March 1, 1928, contained large quantities of rice used in "prebaiting," page 157. Ephemerid nymphs, chironomids and *Pisidium* were present, a single specimen of *Mysis relicta* and a specimen of the Iowa darter, *Poecilichthys exilis*. It was of greater interest to discover that the stomachs contained eggs of the cisco, *Leucichthys artedi*. The eggs were in the eyed stage of development and were present in 5 of the 12 stomachs examined, in an average number of 16 per stomach.

A summary of all the available data indicates that the food of adult whitefish throughout the year in Lake Simcoe is composed of molluscs, 36%, ephemerid nymphs, 30%, chironomid larvae, 16%, caddis larvae, amphipods, hydrachnids, ostracods and fish eggs, 18%.

THE CISCO (*Leucichthys artedi*)

The food of the cisco in Lake Simcoe was determined by an examination of the stomachs of 31 specimens. While the plankton formed the greater part of their food it was noted that as they grew larger the amount of plankton eaten decreased somewhat and the quantity of bottom food increased. On the whole, their food was made up of about 81% plankton (largely of entomostracan forms such as *Bosmina*, *Daphnia*, *Cyclops*, *Diaptomus* and *Senecella*), 11% Ephemeridae, 5% chironomid larvae and 3% other insects, some of them terrestrial. Small numbers of *Pisidium*, oligochaetes, amphipods and ostracods were found in some of the stomachs. The Ephemeridae were mostly in the nymphal stage although in June and July the cisco stomachs contained specimens in which the last nymphal skin covered the future subimago. It is concluded that these individuals were proceeding to the surface for emergence when captured by the ciscoes. At the same season whitefish stomachs contained ordinary nymphs, indicating that the whitefish ate only the Ephemeridae in the bottom mud.

A more striking example of the ciscoes feeding on bottom organisms was found by the writer in Waskesiu lake, northern Saskatchewan, in 1928. In that lake ciscoes less than 25 cm. in length ate 76% Entomostraca and 18% insect larvae, while ciscoes between 25 and 38 cm. in length ate only 25% of Entomostraca and 60% insect larvae. The insect larvae were largely those of *Chironomus plumosus*, which was by far the most important bottom organism in the lake.

THE LAKE TROUT (*Cristivomer namaycush*)

The ciscoes form more than 90 per cent. of the food of the lake trout in Lake Simcoe. The length of the ciscoes captured by the seventeen trout examined ranged from 15 to 25 cm. and as many as six have been taken from a single stomach. Other fish found occasionally in the stomachs of trout are young suckers, the whitefish, perch and the brook stickleback.

The Common Sucker (*Catostomus commersonii*)

The analysis of 27 stomachs of the common sucker has shown that it feeds chiefly on insect larvae. The average composition of the stomach contents was: ephemerid nymphs 49%, chironomid larvae 18%, Mollusca, chiefly Gastropoda, 18%, amphipods 5%, and the remaining quantity, 8%, composed of fish remains, crayfish, isopods and vegetable matter. The gastropods eaten by suckers were chiefly small *Physa* and *Planorbis*, the amphipods all *Hyalella knickerbockeri*.

The Carp (*Cyprinus carpio*)

The examination of carp stomachs is complicated by the large quantity of mud and unidentified debris which obscures the food organisms. In estimating the quantities of the following organisms the percentages are of the total food organisms exclusive of mud and debris. The food from eleven carp stomachs was made up of chironomid larvae 35%, Mollusca, *Physa*, *Lymnaea*, *Planorbis* and *Sphaeriidae* 27%, algae and higher plants 23%, ephemerid nymphs 9%, other insects, amphipods, oligochaetes and ostracods 6%.

The Catfish (*Ameiurus nebulosus*)

The stomachs from four catfish were found to contain *Cambarus* sp. 40%, ephemerid nymphs 36%, fish remains 15%, chironomids, caddis and other insects 9%.

The Perch (*Perca flavescens*)

Three large perch, each more than 3/4 lb. in weight, were found to have fed much like the bass, taking chiefly minnows and crayfish. Most of the perch are smaller and feed chiefly on the insect larvae as indicated by the analyses of 13 stomachs, the contents being composed of ephemerid nymphs 43%, chironomid larvae 5%, other insects, adult and larvae 25%, remains of small minnows 11%, the remainder 16% being made up of crayfish, gastropods, hydrachnids and ostracods.

The Small-mouthed Black Bass (*Micropterus dolomieu*)

The small-mouthed bass feeds upon crayfish and small minnows or young fish. The analyses of 16 stomachs give

the following proportions in its diet: crayfish, *Cambarus* 53%, small fish 29%, dragonfly nymphs 8%, miscellaneous insects, amphipods and gastropods 10%. Since six of these specimens were taken near and in the mouth of the Beaver river where the crayfish is very numerous, it is possible that the average amount of crayfish taken by bass in the open lake is less than 53% of their total food.

THE ROCK BASS (*Ambloplites rupestris*)

Of nine stomachs of the rock bass which were examined, eight were found to contain crayfish. The total contents were composed of crayfish 74%, insect larvae, caddis, Odonata and ephemerid 20%, small fish and terrestrial insects the remaining 6%. Since the rock bass appears to compete with the small-mouthed bass for its chosen food the crayfish, it is fortunate that this species (*A. rupestris*) is not numerous in the lake.

THE LING (*Lota maculosa*)

The contents of twelve ling stomachs were found to be composed of 95 per cent. ciscoes with negligible quantities of chironomid larvae, Mollusca, *Mysis relicta* and Oligochaeta.

In the food of the bottom-feeding fish of Lake Simcoe there are three outstanding constituents, ephemerid nymphs, chironomid larvae and Mollusca. The ephemerid nymphs form a large proportion of the food of bottom-feeders throughout the year. In Lake Nipigon, Clemens *et al.* (1924) found that the Ephemeridae were much more abundant in fish stomachs at certain seasons than at others. In Lake Simcoe this is only partly true. During June and July, when the ephemerids are about to emerge, the stomachs of ciscoes and perch show a larger percentage of mayflies than at other seasons. That these individuals are caught while on their way to the surface is indicated by the fact that most of them are in the last instar with the subimago complete inside the nymphal skin. In the stomachs of whitefish and suckers the quantity of ephemerid nymphs is fairly constant through-

out the year. Since these nymphs are all large in size, it is clear that the duration of the nymphal stage of these burrowing forms over a period of at least two years is of importance in providing a constant supply of large nymphs for the consumption of the bottom-feeding fish. Such a condition would be impossible with a life cycle of one year.

The amounts of the three staple bottom foods eaten by the bottom-feeding fish in Lake Simcoe are shown in table 14.

TABLE 14. Comparing the composition of the more important food organisms of bottom-feeding fish in Lake Simcoe.

	1 White-fish	2 Sucker	3 Carp	4 Perch	5 Catfish	6 Average 1 to 4
Chironomid larvae....	16%	18%	35%	5%	5%	19%
Ephemerid nymphs...	30%	49%	9%	43%	36%	33%
Mollusca............	36%	18%	43%	....	....	18%

In the food of three of the five species shown above the ephemerid nymphs are the most important source of food. For the whitefish they are almost as important as the Mollusca, but the carp, because of its shallow-water feeding habits, is unable to make use of the burrowing nymphs which abound in the deeper water.

Column 6 shows the average amounts of each food organism taken by the four more important bottom feeders. The catfish has been excluded since its numbers are too small to be comparable with those of the other fishes. If it were included the resultant average would be distorted accordingly. In the combined food of the remaining four, the proportions are: Chironomidae 19%, Ephemeridae 33%, and Mollusca 18%. In comparison with the food of bottom-feeding fish we may consider the bottom fauna, which was composed of Chironomidae 64.7%, Ephemeridae 5.8% and Mollusca 18.3% (page 99). The two series are not altogether comparable since in averaging the food requirements of four species we assign equal values to each, which is somewhat

inexact, *e.g.* the whitefish probably outnumber the suckers and their food demands are greater accordingly. The comparison does show, however, a striking difference between the supply and the demand as represented by the fauna present and the organisms eaten. The ephemerid nymphs make up only 5.8 per cent. of the total bottom fauna and yet they supply 33 per cent. of the food of bottom-feeding fish, not to mention those eaten by the ciscoes during the period of emergence. A further reason for the discrepancy between food taken and food supply is to be found in the fact that a part of the fauna is not available as fish food. It has already been noted that the carp do not feed in deep water and are thus denied the larger mayfly nymphs and chironomid larvae. The evidence from fishing in the lake indicates that even the whitefish rarely feed deeper than 30 metres. Accordingly, a considerable quantity of the chironomid and other fauna of the deeper water is not available to them. This condition is most marked in greatly stratified lakes such as those in northern Germany studied by Lundbeck (1926). He found that the "frasszone" or range over which the fish fed was quite limited and that it was cut off fairly sharply at its deeper limit by the oxygen deficiency below the thermocline. In Lake Nipigon, on the other hand, whitefish are known to feed at very great depths, 90 metres or more, the bottom oxygen at these depths being sufficient for their needs. From these considerations it may be seen that a lake with an abundant food supply does not necessarily produce a large quantity of fish since the availability of this food is dependent upon other conditions in the lake.

The composition of the food of three important bottom-feeding fish in various lakes is compared in table 15.

To prevent any ambiguity it may be explained that at the upper left corner of the table, Whitefish, Mollusca 36%, Lake Simcoe, indicates that of the total quantity of food taken by whitefish in Lake Simcoe the Mollusca make up 36%.

The table indicates a considerable variation in the food of the same species in different lakes, a situation which is

TABLE 15. Comparing the composition of the more important food organisms taken by three bottom-feeding fish in four lakes.

<table>
<tr><th></th><th></th><th>Lake Simcoe</th><th>Lake Nipigon</th><th>Oneida lake</th><th>Waskesiu lake</th></tr>
<tr><td rowspan="3">Whitefish</td><td>Mollusca</td><td>36%</td><td>14%</td><td>26%</td><td>23%</td></tr>
<tr><td>Ephemerid nymphs</td><td>30%</td><td>5%</td><td rowspan="2">8%*</td><td rowspan="2">62%</td></tr>
<tr><td>Chironomid larvae</td><td>16%</td><td>28%</td></tr>
<tr><td rowspan="3">C. sucker</td><td>Mollusca</td><td>18%</td><td>20%</td><td>30%</td><td>18%</td></tr>
<tr><td>Ephemerid nymphs</td><td>49%</td><td>20%</td><td rowspan="2">21%*</td><td rowspan="2">68%</td></tr>
<tr><td>Chironomid larvae</td><td>18%</td><td>25%</td></tr>
<tr><td rowspan="2">Perch</td><td>Ephemerid nymphs</td><td>43%</td><td rowspan="2">30%</td><td rowspan="2">25%*</td><td>1.8%</td></tr>
<tr><td>Chironomid larvae</td><td>5%</td><td>53%</td></tr>
</table>

*Insect material of all kinds.

readily explained. In Lake Nipigon, the whitefish food contains a small proportion of ephemerid nymphs because, as indicated by Adamstone (1924), these nymphs are largely confined to the upper 10 metres. As has been mentioned above, the whitefish in Lake Nipigon feed at great depths, eating chiefly *Pontoporeia hoyi*. The quantities of this species, *P. hoyi*, taken in the deep water accounts for the lower proportion of all other bottom foods as compared with Lake Simcoe, in which there are no deep water amphipods. The common sucker, in Lake Nipigon, takes only 20% ephemerid nymphs as compared with 49% in Lake Simcoe where the ephemerids are more abundant. In the food of the perch the two figures, 30% in Lake Nipigon and 43% in Lake Simcoe, show a greater agreement, because in Lake Nipigon the ephemerids are most numerous from 0-10 metres, in which zone the perch are also most frequent.

In Oneida lake the mollusc content of the stomachs is very great as compared with the insect food taken by each of

the three species. This is the direct result of the composition of the fauna, which was found by Baker to be more than 50% Mollusca.

In Waskesiu lake the burrowing mayflies are scarce and the chironomid larvae make up 94% of the total weight of the fauna. As a result of this situation the three species of fish under consideration all eat large quantities of *Chironomus plumosus*, while the ephemerid nymphs are practically negligible as food.

It is evident that the diet of whitefish, sucker and perch is modified, depending upon the availability of bottom organisms. The fact that the larger ciscoes both in Waskesiu lake and in Lake Simcoe take a considerable quantity of bottom food may be regarded as further evidence of this adaptability.

The discussion of fish food may be summarized in the following manner: The bottom fauna of Lake Simcoe provides the major part of the food of whitefish, sucker and carp; it also supplies a considerable quantity of food for the perch, small-mouthed and rock basses and a small part of the food of the cisco.

Of the three staple bottom foods, ephemerid nymphs, chironomid larvae and Mollusca, the latter two are of about equal importance, with the ephemerid nymphs much more important than either. This is surprising in view of the fact that ephemerid nymphs make up only a small percentage, 5.8, of the total fauna.

A comparison of the food of bottom-feeding fish in different lakes indicates that each species of fish is able to exist on very different diets if the fauna makes it necessary to do so.

THE AMOUNT OF NUTRITIVE MATERIALS IN THE DIFFERENT STATES

THE BOTTOM FAUNA

The total quantity of bottom fauna has been calculated and discussed on pages 95-99. The final estimate indicated

that the average dry weight of macroscopic organisms over all depths was 12.38 kgm. per hectare or 1,238 mgm. dry weight per sq. metre. From a chemical analysis of the organisms from thirty dredgings, the total organic nitrogen of the bottom organisms was found to be 7.5 per cent of the dry weight. The total organic nitrogen of the fauna may therefore be expressed as 0.93 kgm. nitrogen per hectare or 93 mgm. organic nitrogen per sq. metre.

The Plankton

The purpose of the plankton investigation was to obtain an estimate of the total plankton present during the summer in order to compare it with the amount of plankton in other lakes and with the other forms of organic matter in Lake Simcoe. With this end in view the samples were taken over the whole period from May to October in order to minimize the effect of minor fluctuations or pulses in the plankton. A number of series of vertical hauls have not been completely examined but as yet they indicate nothing unusual in the vertical distribution of the plankton forms.

Twenty-eight total vertical hauls taken with the 18-inch net (page 27), in various parts of the lake have been weighed and submitted to chemical analyses. About five hauls were taken in each month from May to October inclusive and they were distributed over the 15-20 metre depth zone. Since the average depth of the lake is 17 metres it is thought that these total vertical hauls are quite representative of the plankton in the lake over the five-month period.

The average weight of plankton in the total vertical hauls was 34.5 mgm. dry matter and the average of the total organic nitrogen content was determined as 4.5 mgm. The shape and construction of the net was such that its efficiency, (page 28), was very low, the correction factor being 4.32. The column of water through which the net was drawn had a volume of 106 cubic feet or 3.0 cubic metres. The plankton collected was therefore 11.6 mgm. dry weight per cubic metre. Applying the correction for the efficiency of the net,

the total net plankton throughout the summer is seen to be 50.11 mgm. per cubic metre.

In order to make this value comparable to those given by Juday for Lake George (1922) and for Green lake (1927), the percentage of ash was determined by the method described by Juday (1922, page 44). Representative plankton samples from Lake Simcoe had an ash content of 27 per cent. (dry weight basis) as compared with 32 per cent. in the plankton of Lake George. The difference is apparently due to the larger proportion of diatoms in the plankton of the latter lake. The quantity of dry organic matter in the net plankton of Lake Simcoe is therefore 36.58 mgm. per cubic metre. In Lake George it was 21.2 mgm. and in Green lake 62 mgm. It is seen that the quantities of plankton in three lakes are related in the same manner as their bottom faunas (page 103), *i.e.* Green lake contains the greatest fauna and plankton, Lake George the smallest fauna and plankton. Attention has already been drawn to the fact that Lake George, a smaller but deeper lake than Lake Simcoe, supports a smaller fauna probably because of its greater depth. It would appear that for the same reasons it supports a smaller quantity of plankton.

This correlation between the amount of plankton and the amount of bottom fauna in different lakes is of special interest from three viewpoints:

It is an indication of the essential interdependence of the two groups of organisms.

It throws some light on the question of indices to the richness of lakes (page 142).

It is a confirmation of one of the basic assumptions in the trophic classification of lakes (page 91), *i.e.* that certain lakes are characterized by rich plankton, rich bottom fauna and a low supply of oxygen in the deeper water while others have a scanty plankton and bottom fauna and plenty of oxygen.

Juday (1922) found in examining the plankton of a large number of lakes that the net plankton represents about 1/10 of the total plankton, the remainder being made up of the nannoplankton which may be separated by centrifuging. On

this basis the total plankton of Lake Simcoe from May to October would average about 365.8 mgm. dry organic material per cubic metre. The annual crop as distinct from the amount of plankton present during the summer months is too complex for our present methods of calculation.

THE NITROGEN OF THE BOTTOM OOZE

As an index to the organic content of the bottom ooze and detritus layer, samples were submitted to a chemical analysis which determined the total organic nitrogen. The relation of the amount of nitrogenous material, presumably an indication of the nutritive value of the detritus, to the amount of bottom organisms present in different parts of the bottom of Lake Simcoe, is dealt with in the following section under indices to the richness of lakes. The average amount of total organic nitrogen present in the upper 5 cm. of the bottom deposits in Lake Simcoe was 1.045 mgm. per kgm. dry weight. This is equivalent to 156.7 gm. per sq. metre or 1567 kgm. per hectare.

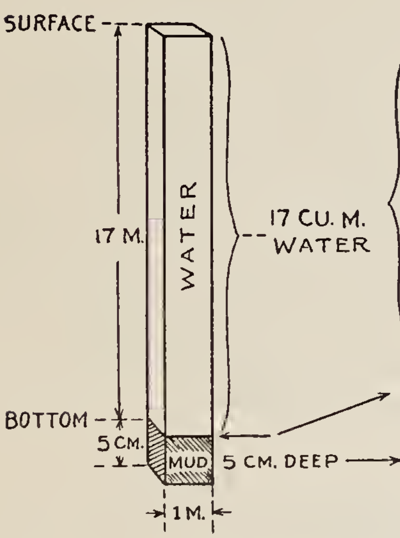
In his investigation of the connecting lakes of the Illinois river, Richardson (1921) found that the mud of the "deeper bottom land" lakes contained 2.7 mgm. organic nitrogen per kgm. dry weight. The mud of shallow weedy lakes contained 3.9 mgm. organic nitrogen. Deep water bottom deposits in Lake Simcoe show an average of 1.04 mg. organic nitrogen per kgm. dry weight.

It is not known what proportion of the nitrogenous material represented by 1567 kgm. organic nitrogen per hectare (1393 lb. per acre) is available as food for the bottom organisms. It is interesting, however, to note the great excess of this organic material over the organic nitrogen content of the macrofauna which amounts to only 0.93 kgm. per hectare (0.827 lb. per acre).

In the aforementioned "deep bottomland" lakes, Richardson found a bottom fauna of 396 kgm/ha live weight, about 79 kgm/ha dry weight. While the life conditions in these lakes are somewhat different from those in Lake Simcoe,

it is noteworthy that the bottom muds contained three times as much organic nitrogen and supported more than six times as much fauna.

Of the states in which organic materials may occur we have still to consider the nannoplankton, the dissolved organic material and the fish. The fish are as yet an unknown quantity but the work of Birge and Juday and their associates has provided a considerable body of data on the other two materials. Their work indicates that the nannoplankton of Lake George collected by a high-speed centrifuge, contained as much as forty times the organic matter of the net plankton. This amount is greater than usual for the nannoplankton in most lakes is from six to ten times the net plankton.



		DRY WEIGHT MGMS.	TOT. ORGANIC NITROGEN MGMS.
1	NET PLANKTON	851·8	83·3
2	NANNOPLANKTON	---	640·0
3	DISSOLVED AND SUSPENDED ORGANIC MATERIALS	---	6000·0
4	BOTTOM FAUNA	1238	93·0
5	DETRITUS & OOZE	---	156,700

DIAGRAM 4

DIAGRAM 4. The vertical distribution of nitrogenous organic matter (exclusive of fish) in Lake Simcoe.

The dissolved and colloidal organic matter in the lake has been shown to make up about 85 per cent. of the total organic matter in the water, the remaining 15 per cent. being made up of plankton (Birge and Juday, 1927). This relation between plankton and total dissolved organic material, and

the former relation between net and centrifuge plankton, are the result of observations on a number of lakes. Applying them to Lake Simcoe may not be fully justified since the lakes from which the relations were derived were all smaller than Lake Simcoe.

Diagram 4 indicates the distribution of organic matter as measured by the total organic nitrogen in a vertical column of water, 1 sq. metre in cross-section and extending from the water surface to a depth of 5 cm. into the mud at an average depth, 17 metres, in Lake Simcoe.

It is seen that the bottom fauna is relatively small, 93 mgm. nitrogen, as compared with the amount of plankton, 723.3 mgm. nitrogen, in the column of water above it. The whole of the living matter, plankton and bottom organisms, 816.3 mgm. nitrogen, is small as compared with the dissolved organic matter of the water, 6,000 mgm. nitrogen, and still smaller as compared with the enormous reserve in the bottom detritus, 156,700 mgm. nitrogen. The amount of organic material in the bottom deposits is perhaps least significant, since we have no means of determining the portion of it which is available for circulation in the nutriment of the lake.

The total amount of organic material present in a lake may be in some measure due to the age of the lake (Pearsall, 1921) and to the nature of its watershed. It is also due to the nature of the life conditions in the lake itself, *e.g.* an eutrophic lake has a greater amount of nutriment in circulation than an oligotrophic lake of a similar size.

SOME FACTORS AFFECTING THE CIRCULATION OF NUTRITIVE MATTER

The circulation of nutritive materials as indicated in diagram 3, page 122, involves three kinds of transformations. The elaboration of organic material by the phytoplankton and other aquatic plants, the feeding of one organism on another or on the dead fragments of another, and finally the decomposition of organic matter.

PLANT GROWTH

In a large lake, such as Lake Simcoe, the rooted aquatic plants are much less important than they are in smaller lakes, (page 89), and the phytoplankton is largely responsible for the conversion of inorganic materials into organic matter. The amount of phytoplankton is necessarily affected by such factors as the temperature, transparency of the water, the length of the growing season and the availability of dissolved nutrient salts. Domgalla and Fred (1926) have shown that the nitrate and free ammonia content of certain Wisconsin lakes decreased in midsummer while the amount of organic nitrogen increased. At this time the algae were most abundant, so that the increase in organic nitrogen was no doubt due to increased photosynthetic action. Rice (1916), after an investigation of the relation of plant growth to nitrogen in Winona lake, concludes that a very small amount of nitrates and nitrites suffice for a flourishing plant growth if the conditions for producing these compounds are present. Birge and Juday (1927) have shown that the organic content of water is usually about ten times as great as the total plankton, so that the bacteria have an abundant supply of nitrogenous materials which may be broken down into nitrates and nitrites.

Domgalla and Fred (*loc. cit.*) have demonstrated the influence of rains and surface water in increasing both the nitrifying and nitrate-reducing bacteria in the water. The whole question of the supply of inorganic nitrogen compounds for plant growth is bound up with the bacteria of the lake. In a lesser degree it is influenced by the inflowing spring and drainage water which have a high nitrate content.

FEEDING ACTIVITIES

Although the growth of phytoplankton is fundamental and essential in the production of food materials for the higher forms of life, the utilization of this fundamental material varies greatly in different lakes. Lundbeck's repre-

sentation of the relation between the three "productions," (page 151), indicates that in deep eutrophic lakes there is a great production of phytoplankton "Urproduktion" and a moderate utilization of this material by the zooplankton and bottom fauna "Zwischenproduktion." In deep oligotrophic lakes the original production of phytoplankton is much smaller, but the degree of utilization more complete, while in shallow lakes of all kinds the utilization of the "Urproduktion" is lowest. The composition of the phytoplankton affects its usefulness as food for minute animals. In certain lakes, usually small, there is a large production of phytoplankton, but it is mostly composed of blue green algae which, instead of providing nutriment, may pile up on shore, decay and produce toxic materials.

Apart from the fact that the bottom fauna feed on the detritus, very little is known of this relation. It has been suggested that the great numbers of micro-organisms and bacteria living in the upper layers of the ooze are an important source of nutriment for the larger bottom organisms.

The availability of bottom organisms as food for bottom-feeding fish is discussed on page 151. In Lake Simcoe the whitefish are thought to feed down to depths of 30 metres, and since 94 per cent. of the total area of the lake is less than 30 metres in depth, most of the bottom fauna is available as fish food. In lakes with more marked stratification the low oxygen supply below the thermocline prevents the fish from feeding in the deep water during a large part of the summer season. In such lakes the upper water is usually very warm so that the bottom-feeding fish are confined to a fairly narrow feeding range (Lundbeck's frasszone, 1926).

The organic material in the food organism is never completely utilized by the individual which eats it, so that at each successive step in the food chain there is a small loss of the organic material manufactured in the original photosynthetic action of the phytoplankton. Schaperclaus (1925) has shown that fish are able to make use of from one-third to one-quarter of the potential food value of bottom organisms, measured as calories.

DECOMPOSITION PROCESSES

Of the nature and rate of bacterial decomposition on the bottom we have comparatively few data. Mention has been made above of the inoculation of the lake water by bacteria brought in by rain and drainage water. The importance and something of the rate of the activity of these bacteria has been studied by Domgalla and Fred (1926), Domgalla, Fred and Peterson (1926) and Rice (1916).

A second factor in the decomposition of bottom materials is the digestive action of such forms as the Oligochaeta and chironomid larvae in the detritus of deep water. Alsterberg (1925) has made a thorough study of the activities of the oligochaetes and compares them with the earthworms as described by Darwin (The Formation of Vegetable Mould through the Action of Worms, 1890). The chironomid larvae are also responsible for some working over of the bottom detritus, but they are more limited in their scope since they have horizontal cases near the surface of the ooze, while the Oligochaeta, as shown by Alsterberg, are able to feed at depths of 3 to 6 cm. below the surface. Since the posterior portion of their bodies projects from the upper surface of the mud (for respiration), a part of the material eaten is brought to the surface. Microscopic examinations have shown that the flocculent material of the upper ooze layer is largely of such "coprogenous" formation.

The loss of organic material through sedimentation is greatest in the polyhumus or peaty type of lake bottom and least in the oligohumus type. In the former the organic materials are incompletely decomposed and the accumulating material is buried and lost in the bottom deposits. The latter type of bottom supports a larger amount of fauna which is more successful in keeping the detritus used up and decomposed. Two main factors tend to prevent the loss of organic materials by sedimentation. The oligochaetes work through the upper 5 cm., devour the organic material and bring some of it back to the surface. The heavier silt, settling to the bottom, sinks through the flocculent detritus which is accord-

ingly left on the surface of the deposit. Even in an oligohumus mud, such as that of Lake Simcoe, there is some loss through sedimentation since layers III and IV contained 0.7 and 0.56 mgm. organic nitrogen per kgm. dry weight, (page 75). These layers are lower than 5 cm. from the surface of the ooze, and the organic material represented by the above quantities of organic nitrogen is probably lost to the circulation of the lake.

INDICES OF THE RICHNESS OF LAKES

The term "richness of a lake" might be applied either to the amount of living matter or the total amount of nutritive material per unit volume. The term "productivity" has been used by various investigators to indicate sometimes the capacity for fish production, sometimes with reference to the total flora and fauna supported by the lake. The capacity for fish production bears no constant relation to the amount of other organisms in the lake as will be indicated on pages 150-152. The following paragraphs contain a discussion of "richness" as indicated by the total organic material in circulation in a lake. The question of fish production is taken up on page 167.

THE PLANKTON

An abundance of plankton is usually associated with an abundant bottom fauna and a low oxygen supply in deep water, while a scarcity of plankton is found in lakes with a scarcity of fauna and a high oxygen content (page 92). The plankton is therefore a general indication of the conditions which we describe as eutrophic and oligotrophic. Further than this, the amount of plankton may or may not be an index of nutritive conditions. In Thienemann's dystrophic lakes the humus content of the mud is the significant feature with the nutritive and oxygen conditions of only secondary importance.

Plankton as an index to richness of a lake is subject to three important limitations.

The quantity of plankton fluctuates greatly during the growth season, due to "pulses" of different organisms. It is necessary to sample the plankton regularly throughout the season if we wish to estimate the total plankton of the lake.

The variation in methods of sampling and analysing makes it difficult to compare the results of different plankton studies. Recent developments in the collection of plankton by centrifuging and in the chemical analysis of the sample will make the data much more comparable in the future.

The quantity of plankton is not always sufficient since the nutritive value varies with the quality of the haul. An overabundance of such forms as the blue green algae may result in decomposition and the production of toxic substances although they represent a richness of organic matter.

THE BOTTOM FAUNA

As has been demonstrated by Lundbeck, Thienemann and others, the quality of the bottom fauna in the deeper water gives some indication of the trophic condition of the lake (page 92). Like the plankton, the amount of bottom fauna varies seasonally, but in the latter case the variation is uniform and not subject to sudden pulses. The difficulty of sampling the large number of dredgings necessary to produce a representative estimate and the variation in methods of recording quantitative statistics all combine to make bottom fauna a difficult method of testing the richness of a lake.

THE ROOTED AQUATIC PLANTS

The amount of rooted and submerged vegetation as an index to the productivity of fish of lakes was suggested by Klugh (1926) in a paper in which he summarizes the available data on the role of such plants in the nutrition of lakes.

The rooted aquatics, especially in small and shallow lakes, play a very important part in sheltering and providing food for animals and in adding to the soluble nutritive materials by their decay. In the larger lakes they

have a much less noticeable effect. In Lake Nipigon, for instance, the great fish production could not be predicted from the scanty vegetation around its shores.

The detritus, as Klugh remarks, receives a contribution from the decay of rooted aquatic plants, but in a lake as large as Lake Simcoe this amount is very small. A microscopic examination of the detritus from the deeper parts of Lake Simcoe revealed an insignificant proportion of allocthonous detritus, produced near shore or on land, as compared with the autocthonous detritus produced in the open water. A larger lake such as Lake Nipigon has still less allocthonous material in its detritus.

It would appear that in large lakes the amount of rooted aquatic vegetation was limited by the shore conditions, since exposed and rapidly shelving shores are unfavourable for plant growth in contrast to shallow, irregular shores which support a heavy growth. In such cases the rooted vegetation could not be proportional to the amount of nutritive material in the lake. At the other extreme, small, shallow and weed-choked lakes may support an enormous invertebrate fauna but few fish, and, as Professor Klugh remarks at the beginning of his paper, "From the practical standpoint the most important consideration in regard to a lake is its capacity to produce fish."

THE ORGANIC CONTENT OF THE WATER

Recent work on small lakes of northeastern Wisconsin (Birge and Juday, 1927) has indicated that the plankton forms on an average about a seventh of the total organic material in the lake water. The average organic content of these lakes was 14.6 mgm. per litre. The authors suggest that the dissolved organic matter, being much in excess of the plankton and fairly constant in quantity, resembles the organic matter of soil which is little affected by the crop which it supports.

Domgalla and Fred (1926) show that in five lakes near Madison, Wisconsin, including Lake Mendota, the total

organic nitrogen varies between 0.6 and 1.4 mgm. per litre throughout the season. The inorganic nitrogen in the form of nitrates and free ammonia was usually about 0.25 mgm. per litre. While the plant growth used up some of this inorganic material at midsummer and caused an increase in the organic nitrogen, this exchange involved only a small quantity, roughly one-fifth, of the total nitrogen of all kinds in the water.

Birge and Juday (1927) demonstrated that the plankton showed a fairly constant relation to the total organic matter in the water. In more than one-half the lakes studied the plankton was between 10 and 20 per cent. of the total organic matter.

The available data suggest the possibility of the organic content of the water as a satisfactory index to the richness of the lake as a whole, though the condition in large lakes has not been investigated. In small lakes the total organic material in the water appears to be fairly constant and closely related to the plankton fauna which the lake supports.

THE ORGANIC DETRITUS

The detritus has been shown in diagram 3 (page 122), in a central position among the four other states of nutritive matter, a position which indicates something of the actual relations existing between these materials. The detritus is partly dependent on the plankton for its derivation; it provides food for the bottom fauna and, in its decomposition, dissolved organic and inorganic nutritive matter is returned to the water. Is it possible that the richness (organic content), of the detritus is indicative of the general richness of the lake?

In lakes of a dystrophic type (page 92), the bottom fauna has been found low in quantity and with little relation to the high organic content of the bottom deposits. The high degree of humosity or peaty nature of the bottom is unfavourable for the bottom fauna. In the oligo- or eutrophic types the bottom fauna production and plankton are respectively poor

and rich but the bottom fauna is limited less by the available food supply (detritus), than by the oxygen content of the deeper water. It is therefore unlikely that in any of these types the amount of organic detritus on the bottom will provide an index to the amount of life in the lake.

A preliminary experiment to determine the relation of the nutritive material in the bottom deposits to the amount of bottom fauna was carried out in Lake Simcoe during 1927 and 1928. Bottom fauna samples were taken with the dredge and screened as described on page 16. The weight of the organisms from each dredging was determined by drying and weighing rather than by calculating on a basis of average dry weight per individual, which was the method employed in the general survey.

The bottom materials were collected with the heavy sampler and determination of the total organic nitrogen were made by the Kjeldahl method on the material from the upper 5 cm. of the mud. A dredging and a sample of bottom material were taken simultaneously at each of twenty-six stations at depths of 11 to 34 metres in widely scattered parts of the lake. The data from these samples are presented in table 16 along with the date of sampling.

The samples were taken mostly in May and June in order to reduce the error resulting from seasonal variation in the amount of bottom fauna. While the relation between amount of fauna and the organic content of the ooze is not readily seen from the table, the same data, presented as graph XI, indicate that the two quantities vary in an inverse ratio. In other words, those places in which the organic nitrogen is high support a smaller fauna than locations in which the organic nitrogen is low. That several of these points are far from the curve is not surprising in view of the error inherent in the sampling of bottom fauna (page 18), and the variation in individual dredgings taken from one locality, (page 19). At twenty-one of the twenty-six stations the correlation between bottom fauna and the amount of nitrogen was quite marked.

Certain analyses were made to test the method of samp-

TABLE 16. Showing the depth, the amount of bottom fauna and the nitrogen present in the ooze at twenty-six stations in Lake Simcoe.

Station no.	Depth in metres	Date	Bottom organisms per 500 sq. cm.		Total organic nitrogen upper 5 cm. of mud p.p.m. dry weight
			Dry wt. mgm.	Total org. nitrogen mgm.	
1	19	May 28	57	3.44	0.97
2	19	"	26	2.28	1.07
3	17	"	35	2.00	1.08
4	17	June 30	74	3.76	0.82
5	13	"	42	3.00	1.02
6	33	"	35	3.40	1.08
7	30	Sept. 22	16	1.32	1.11
8	21	Aug. 3	46	3.40	1.04
9	28	May 16	40	2.85	1.02
10	31	"	10	1.95	1.20
11	32	"	60	3.20	1.05
12	34	May 17	30	....	1.19
13	34	"	40	....	1.70
14	40	"	40	2.42	1.95
15	20	May 19	20	....	1.50
16	38	"	50	2.91	0.86
17	38	May 21	30	2.7	1.15
18	38	"	20	2.4	1.10
19	37	May 23	40	2.8	1.10
20	37	"	60	2.73	0.90
21	34	"	43	2.65	0.95
22	28	"	40	....	0.60
23	14	May 24	22	....	1.05
24	15	June 6	20	....	0.40
25	15	" 7	110	4.38	0.60
26	11	" 20	105	3.9	0.85

ling the bottom deposits and to indicate the nature of the organic material present. These results are to be considered before proceeding with the discussion of the reasons for the inverse relation indicated above.

The samples of bottom material from the deeper water were taken from the upper 5 cm. of the core brought up by the heavy sampler. This depth was chosen since it roughly

corresponds with layers I and II (page 73), in which most of the organic detritus is found. Table 6 on page 75, indicating the distribution of total organic nitrogen in the various strata of the bottom deposits, shows that layers I and II include the part of the deposits which is richest in organic matter. The nature of the organic nitrogen was determined by a further analysis of four samples, the composition of which is shown in table 17.

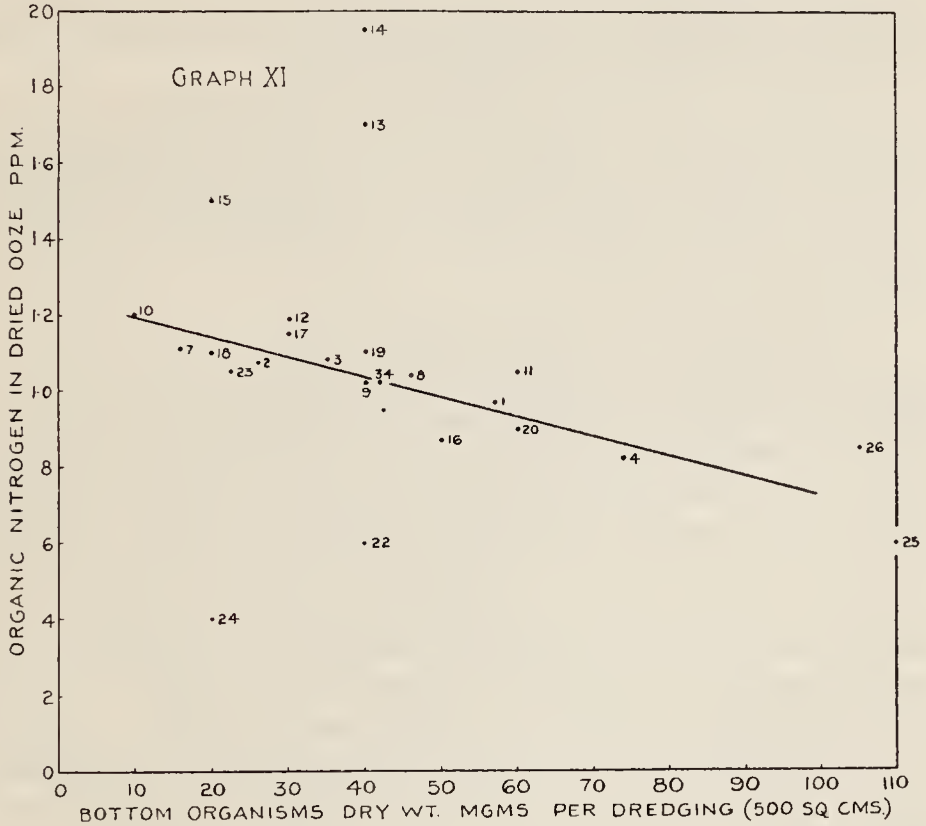
TABLE 17. Showing the nature of nitrogenous materials in the bottom ooze.

Sample	Per cent. moisture	Amounts of nitrogen expressed in p.p.m. dry weight				
		Total N:	Free ammonia	Albuminoid ammonia	Nitrates	Nitrites
1.......	83.6	0.847	0.052	0.647	0.00012	trace
2.......	85.4	1.066	0.052	0.526	0.00024	0.000012
3.......	82.5	1.020	0.039	0.558	0.0003	0.00003
4.......	70.0	1.080	0.012	0.816	0.0009	0.000042
Average	80.4	1.003	0.039	0.637	0.0004	0.000021

Having indicated in a general manner the nature of the nitrogenous materials in the bottom ooze, we may return to the relation between this material and the bottom fauna.

As indicated in graph XI, a large fauna is found where the organic nitrogen content of the detritus is small, and vice versa. It might appear that where the bottom fauna was abundant the greater number of organisms were able to eat a large proportion of the detritus while a smaller fauna required less food and allowed the detritus to accumulate. This, however, would not be a stable condition since, if no other factor was limiting, the organisms would tend to increase or decrease to reach an equilibrium with the available food supply. It is therefore probable that some factor, other than food, limits the abundance of bottom organisms, giving rise to richer and poorer communities, after which the inverse ratio of fauna to food can be explained as suggested above by the greater or lesser consumption of the available food supply.

Frequent mention has been made of the uniformity of the bottom in the deep water of Lake Simcoe, and under these apparently uniform conditions it is difficult to suggest any factor which would account for an irregular distribution of the organisms on the deeper part of the lake bottom. Since the oxygen supply of the lower water has a marked effect on



GRAPH XI. The relation between the amount of organic matter in the bottom ooze and the amount of fauna at twenty-six stations in Lake Simcoe.

the distribution of bottom fauna (page 84), it may be suggested that the "other factor" which is responsible for minor fluctuations in the density of the fauna, is the oxygen supply on the surface of the mud. In order to test this possibility, a method of sampling the water at the surface of the mud must be developed since the "microschichtung" phenomenon, (page 84), makes the usual determination of bottom oxygen

quite inadequate. It is also possible that currents might affect an irregular distribution of bottom organisms either through unequal distribution of the oxygen supply, through unequal distribution of detritus or more directly through their effect on the distribution of eggs or larvae of aquatic insects.

It should be mentioned that the amount of nitrogenous detritus, as indicated in table 16, showed no correlation with the depth at which the sample was taken.

From the above consideration it would seem that, although the organic material in the bottom detritus is largely derived from the plankton and serves as food for the bottom organisms, the amount of organic material in the detritus is not always indicative of the amount of life a lake can support.

A consideration of the possible indices to the richness of lakes has led to the conclusion that there is as yet no absolute criterion, although certain indicative conditions can be more easily examined and result in more useful information than others. For instance, a single determination of the oxygen in the deeper water of a lake at midsummer might show that the lake was eutrophic and suggest the usual features of a eutrophic lake, *i.e.* rich plankton and bottom fauna. The occurrence of the larvae of a single species of chironomid on the bottom mud might give the same information. In most cases it is still necessary to examine several features such as the plankton, bottom fauna, detritus, bottom temperature and oxygen before arriving at any conclusion as to the richness of the lake.

FISH PRODUCTION AS RELATED TO BOTTOM FAUNA

The relation between fish production and bottom fauna had been investigated only in small ponds until Alm (1922), correlated these features in fifteen lakes of southern Sweden. He designated the relation of fish caught per hectare to live weight of bottom fauna per hectare as the **Fb** coefficient. As might be expected, the **Fb** coefficient varied greatly in dif-

ferent lakes, but Alm was able to demonstrate that most of the variations could be correlated with the type or condition of the lake. As a result of his work he distinguished three types among the fifteen lakes studied.

	No. of lakes	Maximum depth	Average bottom fauna, live wt.	Average Fb coeff't.
1. Deep lakes with high coefficient..............	5	18-98m.	7 kgm/ha	1:3.6
2. Lakes of moderate depth with low coefficient....	4	8-14m.	60 kgm/ha	1:17
3. Shallow lakes with high coefficient..............	6	2-6m.	60 kgm/ha	1:2.5

In these lakes the lowest coefficient was 1:31, in a small lake 8 metres deep with a *C. plumosus* type of fauna. The highest coefficient, 1:0.8, was found in a lake 30 metres deep with a *Tanypus* fauna, and a second very high coefficient, 1:0.9, in a large lake 2.5 metres in depth and a fauna in which *Corethra* larvae were predominant.

Alm's work indicated that the deep lakes with a high coefficient had either oligochaete or *Tanypus* types of fauna; the other two classes showed no correlation between type of bottom fauna and Fb coefficient. A further observation was that the lakes with a smaller quantity of bottom fauna usually had higher coefficients.

Lundbeck (1926) relates the fish production to the bottom fauna and carries the relation further to "Urproduktion" which is the contribution of plants to the nutritive matter of the lake, both by building up organic material and by their decomposition products. The bottom fauna he mentions as the chief component of the "Zwischenproduktion" and the fish as the "Endproduktion." The theoretical relation between the original, intermediate and final productions in different lakes is shown by Lundbeck (1926*a*, page 54) to be as follows:

	Urproduktion	Zwischen-produktion	Endproduk-tion
1. Deep eutrophic lakes (rich in food, poor in O_2)..........	100	40	25
2. Deep oligotrophic lakes (rich in in O_2, poor in food)........	100	85	60
3. Shallow lakes of all kinds.....	100	20	20

Although the deep oligotrophic lakes show the most complete utilization of the Urproduktion, the amount of this fundamental plant-produced nutriment is small in the oligotrophic type of lake so that the final result is a smaller production of fish in an oligotrophic lake than in either of the other two types.

In order to make a more accurate correlation between the food value of the bottom fauna and its utilization, Schaperclaus (1925) and others have made use of the caloric value of the bottom organisms in calculating the rate at which the bottom fauna is utilized by fish and the loss in energy entailed in this transfer. While this work has at present no economic application, it is tending towards an accurately determined **Fb** coefficient based on the yearly production of bottom fauna which will be of great value in estimating the fish-producing capacity of a lake.

The utility of the **Fb** coefficient as yet is subject to several limitations. It does not directly consider the plankton-feeding fish nor the species which we do not catch. For instance, Lake Simcoe has a large population of perch, ling and suckers, very few of which are ever taken in fishing. It is also clear that the fish caught per year may be greater or less than the annual production. Over a short period a high **Fb** coefficient might indicate only overfishing or a low **Fb** might show either low production or incomplete utilization of the crop.

The value of the **Fb** coefficient is in the provision of even a rough method of comparing the fish production of lakes and in calling attention to the differences in capacity for fish-

production as dependent on nutritional factors, depth, and other physical and ecological conditions in the lake.

In Lake Simcoe the average catch of fish during the past sixty years has been about 130,000 lb. per annum, valued at at $9,000 (page 166). Estimating the live weight of the bottom fauna as 55 lb. per acre (live weight is approximately five times dry weight), this represents an **Fb** coefficient of 1:75. For the period from 1868-1908, the average fishery of 50,000 lb. per year is represented by an **Fb** of 1:200. For the period from 1908 to 1928, the average catch was 234,000 lb. and the **Fb** 1:42; and for the same period the average catch in deep water, 10 to 45 metres, was 19,000 lb., which for an area of 200 square miles represents the extremely low coefficient of 1:310. In the shallow water (1-10 metres) the **Fb** coefficient was for the same period, 1:15.

The lowest coefficient found by Alm was 1:31, which is higher than the present value for Lake Simcoe. It is quite evident that the crop of fish taken from Lake Simcoe is very low, especially in the deeper water where the **Fb** coefficient is only 1:310. The value would suggest that the productive capacity of this area was not being properly utilized, a point which is further discussed on page 167, part III.

SUMMARY OF PART II

The circulation of food materials is summarized in diagram 3 (page 122), which shows the nutritive material of the lake divided into five states and indicates something of the way in which materials are transformed from one state to another.

The bottom organisms in Lake Simcoe form the major part of the food of whitefish, suckers and carp, as well as much of the food of perch and bass and a small quantity of the food of the ling and the cisco. The chief bottom-food organisms are the ephemerid nymphs, Mollusca and chironomid larvae, the ephemerid nymphs being unusually important in view of their small numbers as compared with other bottom organisms.

A comparison of the amounts of nutritive material present in different states indicates that the total plankton is about eight times as great as the bottom fauna per unit area. The living organic matter in the form of plankton and bottom fauna is small, about 0.5 per cent., in proportion to the amount of organic matter present in the water and the upper 5 cm. of the bottom deposits.

Different lakes vary in the amount of phytoplankton "Urproduktion" which they support, in the extent to which this material is utilized to produce zooplankton and bottom fauna "Zwischenproduktion," and in the extent to which the zwischenproduktion is used to produce fish "Endproduktion." These variations have been shown to depend in some measure on the depth and trophic condition of the lake.

No one feature of the life or life conditions in a lake will provide an absolute index to its richness, (amount of nutritive material present). The various indices—bottom fauna, plankton, organic content of the water, rooted aquatic plants, bottom oxygen, etc., vary greatly as to their utility and the ease with which they may be determined.

The **Fb** coefficient, relation of fish caught to bottom fauna present per unit area, is as yet not wholly satisfactory, but it is of some value in providing a limited method of comparing the crop of fish taken from lakes, and is of greater value in calling attention to the fact that certain factors, such as depth and trophic condition, are responsible for variation in the productive capacity of lakes. The extremely low **Fb** coefficient in Lake Simcoe is thought to indicate a very incomplete utilization of its possibilities, especially in the deeper water.

PART III

THE FISHERIES OF LAKE SIMCOE

THE HISTORY OF FISHING IN LAKE SIMCOE

On August 17, 1615, Champlain led a band of Huron warriors across the narrows between Lake Simcoe and Lake Couchiching and on into the territory of the Iroquois. In his journal for that date, he mentions an Indian fishing station at the outlet of the lake where the village of Atherley now stands. In 1891, Wallace, of Orillia, records the discovery of the remains of a Huron fish weir in the Narrows and suggests that it was the one referred to by Champlain in his journal.

In 1687, Lahontan's "La Grande Voyage" tells of Iroquois hunting and fishing trips in the direction of Lake Taranto (Simcoe), a district in which they were free to wander, having massacred its Huron population in the years 1649-50. In the next hundred years there is very little record of fishing in the lake, although the Algonquins were known to encamp along its northern and western shores, while the Ojibways who followed them in occupying the Simcoe district were expert fishermen.

Sir Geo. Head spent the spring of 1814 on Kempenfelt bay, and in his "Forest Scenes in Canada," (pub. 1838) he describes in detail the fish and fishing methods of the locality. With the sum of nine dollars and a quantity of whiskey he was able to buy from an Indian a complete fishing outfit, consisting of a bark canoe and a fifteen-foot spear with two barbed iron spikes. During his stay he speared numbers of salmon (lake trout), carp (suckers), perch, bass, freshwater herring and a large catfish. He confessed that "like all their freshwater brethren," the fish of Lake Simcoe were inferior in quality to those of the salt water.

Smith's Canadian Gazetteer in 1846 testifies to the excellence of Lake Simcoe maskinonge and whitefish, and in

1852, after a trip to the Orillia district, Mrs. Jameson praises the quality of the bass. A description of the Northern Lakes of Canada, by Barlow, 1886, tells of bass, trout and maskinonge fishing, all of which indicate that Lake Simcoe received early recognition as a fishing ground.

In 1868 we have the first statistical record of fishing in Lake Simcoe, when trout, whitefish and ciscoes were taken to the value of $2,450. An analysis of the fishing records for the last 60 years will be found on page 165.

Statements made to the Dominion Fisheries Commission (1893) by residents of the district indicate that the numbers of whitefish and trout had become considerably reduced at that time.

Angling for bass in Lake Simcoe became more intensive as large numbers of summer homes sprang up around its shores. Residents around the lake say that the peak of this fishing was about 1905, after which the numbers of bass fell off rapidly. At the present time the bass are not heavily fished due to their scarcity. The maskinonge have practically disappeared and the trout, although present in moderate numbers, are difficult to catch. The causes of this depletion, including the introduction of carp, will be discussed in the following pages.

FISHING METHODS IN LAKE SIMCOE

In Lake Simcoe, several unusual methods are employed in angling and in commercial fishing, in addition to those in common use in other lakes.

Angling for Ciscoes in the Mayfly Season

During the swarming of the Ephemeridae* in Lake Simcoe, it is found that the cisco, *Leucichthys artedi*, becomes a surface-feeder for a ten-day period. The common species of *Ephemera*, *E. simulans*, swarms about June 27-30, while

*The Ephemeridae or mayflies are known to the fishermen as shadflies, bass flies and fish flies. Anglers use the less familiar terms of "Duns" for the subimago and "Spinners" for the adults.

the large *Hexagenia*, *H. occulata*, reaches its maximum emergence about July 1st. At the latter date, ciscoes can be taken in great numbers in certain parts of the lake, notably in the Narrows at Atherley. Plate IV, fig. 1, shows a "fleet" of boats on the bay at Atherley on July 1, 1928, the occupants being engaged in this sport. The newly emerged adult or subimago of the large mayfly, Hexagenia, are the chief bait, although the fish are readily taken on a suitable artificial fly. A catch of 60 ciscoes, (plate IV, fig. 2), in two hours is not an unusual record for a fisherman on this area or even from the dock at Atherley. The fish continue to rise for about ten days although the fishing is usually best during the first three days in July.

ANGLING FOR WHITEFISH WITH MINNOWS AS BAIT

Whitefish in other waters are occasionally taken on a hook, usually when fishing for some other species. In Lake Simcoe the method is so widespread and successful that it has become a commercial practice in certain seasons.

Most of this fishing is carried on in depths of 15 to 75 feet of water through holes cut in the ice. Each fisherman is provided with a lightly-constructed fish-house, Plate V, fig. 1, about 3 ft. by 5 ft. by 4½ ft. high, which can be easily moved over the ice on a hand-sleigh. The houses are windproof and each is provided with a small stove so that the fisherman may sit comfortably inside. Catches of 50 to 75 whitefish in a day are considered good fishing. The modern fisherman uses his automobile to reach the fish-house, which may be three to five miles from shore.

The minnows which are used for bait are chiefly the lake shiner, *Notropis atherinoides*, about two inches long. They are kept alive all winter by confining them in a cage which is sunk in ten feet of water at the end of a convenient dock. Salted minnows of the same species are used for prebaiting, *i.e.* a small pailful is scattered over the bottom where the fisherman places his house. If live minnows are scarce, salted ones are used for bait, and for prebaiting, chopped ling flesh, cooked rice, wheat and other grains are considered equally

good. The prospective fisherman usually spares himself any such expense by salting down in the previous autumn as much as one or two hundred pounds of minnows, caught with a dip net usually at the entrance to a boathouse.

The extent of this winter-fishing is indicated by the observation that 70 fish-houses were located within a two-mile radius of Jackson's point in March, 1928. During January, February and March of the same year, one dealer bought more than nine tons of whitefish (16,000 fish) from about 15 men engaged in this kind of fishing.

It has been found that whitefish can be caught with minnow bait on certain shoals, 20 feet to 30 feet deep,from November 5 until the ice forms on the lake and in the same places in the early part of May. One enterprising fisherman at Beaverton finds that by prebaiting and marking the spot with a buoy, he is able to catch whitefish all summer, using live minnows for bait.

While this method is used primarily for whitefish, an occasional ling, cisco, perch and sucker is caught with the same tackle.

SPEARING TROUT THROUGH THE ICE

Making use of the fish-houses described above, the fishermen are able to spear trout throughout most of the winter. The house is light proof and banked with snow around its edges, so that the fisherman is able to see 25 to 40 feet into the water, depending on its turbidity and on the amount of snow covering the ice. A cleverly-constructed decoy (Plate V, fig. 2) is made of white wood with bright metal fins, the appearance and size of the device being that of the cisco. The decoy is so balanced and the fins so turned that by an intermittent pulling on the line the imitation cisco is made to travel in a circle about 10 feet in diameter. Following the decoy, the trout is lured upwards into striking distance of the fisherman's 16-foot spear. A less common method makes use of a similar decoy with hooks attached, Plate V, fig. 2, in which case the trout is allowed to strike the lure in deep water.

During the past four years, trout-fishing through the ice has been so unsuccessful that many of the fishermen have given it up and now confine their attention to the whitefish.

The fishermen are allowed to sell their catch of whitefish or trout though it is necessary to obtain a licence before using a spear. The bulk of the commercial fishing in the lake is provided by the carp. Carp are taken in the weedy bays with heavy seines, 200 to 400 yards in length and 15 to 20 feet deep at the centre. The only legal gill netting in the lake is carried on by the Indians of the Georgina island reserve, who are allowed the special privilege of using a gill net for their personal needs.

THE FISHES OF LAKE SIMCOE

The following annotated list of fishes includes those forms taken in the lake during the course of the survey, with the addition of three species recorded by Meek (1902) and the rainbow trout. The list includes 31 species and is probably incomplete since the systematic study of the fish was accessory to the main investigation. The identification of the specimens has been verified by Professor J. R. Dymond of the University of Toronto.

The food of the larger fishes of Lake Simcoe has been dealt with in Part II, pages 125-133.

1. *Coregonus clupeaformis* (Mitch.)

The common whitefish of Lake Simcoe is abundant but of small size. The average weight of several thousand taken in 1928 was 1 lb. 2 oz., while a fish of 2½ lbs. weight is quite unusual. Spawning occurs between November 5 and 25, on stony shoals from 6 to 15 ft. deep.

2. *Leucichthys artedi* (Le Sueur)

The cisco of Lake Simcoe differs in a number of respects from the typical *artedi* of the Great Lakes. The fishermen of the lake distinguish a small slender form, ½ to ¾ lb., as

"trout herring," in contrast with the larger specimens, "blue backs," ¾ to 1 lb., although specimens of an intermediate character are to be found. They are said to spawn in mid-November along with the whitefish.

3. *Salmo gairdneri* Rich.

The rainbow trout was planted in the lake in 1918 (20,000) and again in 1922 (5,300). There is at least one authentic record of a 5-lb. rainbow trout caught near Orillia in the summer of 1924. Several other reports were probably reliable, but not thoroughly substantiated.

4. *Cristivomer namaycush* (Walb.)

The lake trout is still numerous in Lake Simcoe but during the past five years there has been a noticeable decrease in the numbers taken by trolling. The average size of those taken is about 5 lbs. with occasional specimens of 12 to 14 lbs., and the largest known record a 28-lb. trout taken in 1909. It has been observed that trout taken on the west side of the lake, mostly in the vicinity of Eight Mile point, average 2½ to 3 lbs., while those taken in the east, off Thorah and Georgina islands, are larger, averaging 6 to 7 lbs. Spawning is said to extend from October 15 to November 1, spawn being deposited among the larger stones on shoals in from 10 to 25 ft. of water. The food of the trout is practically all made up of ciscoes, with only an occasional whitefish or young sucker.

5. *Catostomus commersonii* (Lac.)

The common sucker is both large and numerous in the lake. The average weight of specimens taken during the experimental work was 2¾ lbs., but many were as large as 3½ lbs.

6. *Cyprinus carpio* L.

The carp is now one of the most abundant fish in the lake and supports the only commercial fishery of importance. It reaches a large size, many of those taken by the seine weighing as much as 12 lbs., while a 20-lb. carp is not unusual.

The carp is thought to have been introduced into Lake Simcoe through the Holland river into which it had escaped when a mill dam near Newmarket broke about 1896. Fishery overseer Terry of Lake Simcoe district, in his report for 1899, states that "Great numbers of carp have made their appearance in the Holland river and in the marshes of Cook's bay." The spread of carp in the lake was very rapid and in 1911, when the first intense fishing was begun, fishermen using two 400-yard seines were able to take 462,400 lbs. of carp in one year. In 1927, an epidemic of an unknown nature among the carp of the lake killed off a considerable number of all sizes. The reports of the mortality were greatly exaggerated for there was no observed decrease of carp in the following season.

7. *Rhinichthys atronasus lunatus* (Cope)

The black-nosed dace was not taken during the survey but Meek (1902) records it as common at Hawkestone.

8. *Rhinichthys cataractae* (Cuv. & Val.)

The long-nosed dace was common at Beaverton and at the Narrows, Atherley.

9. *Semotilis atromaculatus* (Mitch.)

Creek chub are not common in the open lake but are found in large numbers in the mouths of streams.

10. *Pfrille neogaeus* (Cope)

A number of small specimens of this minnow were taken in a seine haul in the Narrows at Atherley.

11. *Notropis heterolepis* Eig. & Eig.

The black-nosed shiner, or Muskoka minnow, was taken in comparatively small numbers. Meek (1902) records it at Hawkestone.

12. *Notropis hudsonius* (Clinton)

The spot-tailed minnow is moderately abundant and reaches a fair size, 3 to 4 inches, in Lake Simcoe. Several of

the specimens taken had the larva of a large cestode, *Ligula sp.*, in the visceral cavity.

13. *Notropis atherinoides* Raf.

The lake shiner is the most abundant minnow of the lake although it is comparatively small, averaging about 2 inches in length. It supplies the major part of the whitefish bait for which purpose it is salted away in great quantities every autumn. Other minnows occasionally found in this bait material are *N. hudsonius*, *N. cornutus*, *Chrosomus erythrogaster* and *Hyborhynchus notatus*.

14. *Notropis cornutus* (Mitch.)

Small specimens of the common shiner were taken in moderate numbers in shallow water.

15. *Hybognathus nuchalis* Agassiz

The silvery minnow is recorded by Meek as abundant at Hawkestone.

16. *Chrosomus erythrogaster* Raf.

The red-bellied dace was taken in large numbers at Beaverton and scattered specimens were taken along the south and western shores of the lake. Most of the specimens were not more than 1½ inches long.

17. *Hyborhynchus notatus* (Raf.)

The blunt-nosed minnow occurred in moderate numbers at Beaverton and Atherley.

18. *Pimephales promelas* Raf.

Although the fathead was taken only in small numbers, Meek has recorded it as abundant at Hawkestone.

19. *Ameiurus nebulosus* (Le Sueur)

This is the common bullhead or catfish of the lake. In certain features the specimens tend to resemble *A. melas*. Hubbs, in a recent paper, suggests that in the northern part of its range *A. nebulosus* varies towards *A. melas*.

There are several records of very large catfish caught in Kempenfelt bay, Jackson's point, and at Gamebridge. A 19¾-lb. specimen was speared by A. Grew off the dock at Jackson's point in 1923, this being, to my knowledge, the largest authentic record. It is unlikely that these specimens were *A. nebulosus* since the largest recorded size for this species is only 19 inches.

20. *Esox masquinongy* Mitch.

The maskinonge was at one time abundant in Lake Simcoe. At present a few specimens are taken each year in Cook's bay and in the Holland river, while at infrequent intervals specimens are reported from the Black and Talbot rivers.

The absence of the pike, *E. lucius*, is a remarkable and as yet unexplained feature of the fish fauna of Lake Simcoe. It occurs in other waters of the Trent canal system, both above and below Lake Simcoe, a few specimens being taken as near as the north end of Lake Couchiching.

21. *Fundulus diaphanus menona* (Jord. & Copeland)

Meek records this species at Orillia.

22. *Percopsis omisco-maycus* (Walb.)

Trout perch were taken in several parts of the lake.

23. *Perca flavescens* (Mitch.)

The yellow perch is by far the most abundant of the spiny-rayed fishes in the lake. In the shallow water great numbers of small perch are to be seen and in the deeper water large specimens, more than 1 lb. in weight, are taken in gill nets or with bass tackle.

24. *Stizostedion vitreum* (Mitch.)

The pickerel is exceedingly rare in the lake, most of the inhabitants denying its presence. A few specimens were taken in the north-eastern part of the lake ten to fifteen years ago. The absence of this species is as inexplicable as that of

the pike, since like the latter, the pickerel is found in Lake Couchiching and the Severn river, with no barriers between these waters and Lake Simcoe. One and one-half million pickerel fry were planted in Lake Simcoe in 1922-24 with no apparent effect on the fauna of the lake.

25. *Percina caprodes* (Raf.)
Large numbers of log perch were taken in seine hauls in various parts of the lake.

26. *Poecilichthys exilis* (Girard)
The Iowa darter was the only other representative of the darter group taken during the survey. It was most common in the vicinity of Beaverton.

27. *Micropterus dolomieu* Lac.
The small-mouthed black bass is the important game fish of the lake. Its average weight is about 2 lbs., with occasional specimens of 4 or 4½ lbs. in weight.

28. *Eupomotis gibbosus* (L.)
The pumpkin seed, or sunfish as it is locally termed, is widespread but not numerous in Lake Simcoe.

29. *Ambloplites rupestris* (Raf.)
The rock bass although more numerous than the pumpkin seed, is very much less abundant than the perch. It seldom exceeds a weight of one-half a pound.

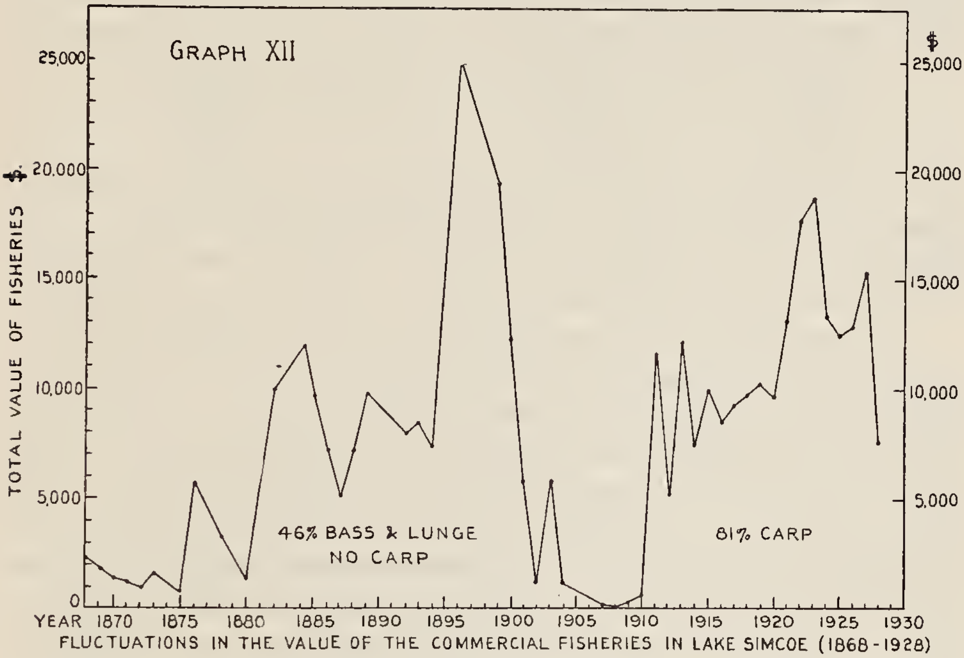
30. *Eucalia inconstans* (Kirt.)
The brook stickleback is widely distributed around the shores of Lake Simcoe, though its numbers are small.

31. *Lota maculosa* (Le Sueur.)
The ling is abundant in the lake and reaches an average weight of 4 to 5 lbs. Living in the deep water and feeding on the cisco, it is an important competitor of the lake trout.

STATISTICS OF THE LAKE SIMCOE FISHERY

Records of the commercial fishing in Lake Simcoe have been obtained for the early years from the annual reports of the Dominion Department of Marine and Fisheries and for the later period from the annual reports of the Ontario Department of Game and Fisheries.

To indicate the fluctuation in the fishery of Lake Simcoe, Graph XII has been constructed, showing the value of the



GRAPH XII. Fluctuations in the value of the commercial fishery in Lake Simcoe (1868-1928).

commercial fishery over the last sixty years. The minor annual fluctuations are largely the result of variation in the number of fishermen and in the amount of equipment and as such they may be disregarded in our general consideration. The curve shows in general an increase in the fishery from 1870 to 1896, after which time it fell off rapidly till in 1908 the fish taken were so few as to be practically valueless, $91.00. This decrease was in part due to the prohibition of the sale of

game fish brought about by an order-in-council in the year 1903. From 1910 to the present time, the fishery varies about a mean value of $10,000 per year. The minimum fishery in 1908 separates two fairly distinct periods, which will be considered separately.

The period of forty years, 1868 to 1908, had an average fishery valued at $9,000. The total weight of the catch was made up of 28% lake trout, 27% bass, 19% maskinonge, 15% whitefish, and 11% ciscoes and coarse fish. The following statistics indicate the large quantities of game fish taken out during this period:

1896—Bass	78,000 lbs.,	Maskinonge	17,800 lbs.
1899— "	43,000 "	"	27,000 "
1900— "	70,200 "	"	16,800 "

Over the whole forty years the bass and maskinonge made up about 46% of the total weight and value of the catch. In short, the period may be described as one of increasing exploitation of the game fish.

An analysis of the statistics for the second period shows a very different condition. The average value of the fishery has increased a little, being now $10,000 per year. The total weight of fish taken is composed of 71% carp, 18% perch and coarse fish, 7.1% trout, 2.6% whitefish, 0.8% cisco. Of the total value of the fishery, the carp makes up 81%, as indicated in the graph. The decrease in 1928 may be due to an epidemic among the carp during the first week of August, 1927. The effect was chiefly felt through the market since the carp did not appear to have suffered any appreciable decrease in numbers.

The graph, in illustrating the fluctuation in value of the fishery, tells only a part of the story. During the first forty years the total weight of fish caught was roughly 2,200,000 lbs., an average of 55,000 lbs. per year, and the annual value was $9,000. During the last twenty years the total catch has been about 4,679,000 lbs., an average of 233,950 lbs. per year and the average annual value has been $10,000. It is seen that even with the quantity of the catch increased to four times what it was in the first period, and with the value of

fish slightly increased, the decrease in the quality of the fish fauna was so great that the resultant value of the fishery increased only 10 per cent. In other words, the market value of the carp, 81 per cent. of the present catch, is less than one-quarter that of the bass, maskinonge and trout which made up the catch between 1868-1908.

The graph should not be interpreted as indicating a cessation of bass and maskinonge fishing about 1902, nor a rapid increase in the numbers of carp in 1910. The figures do show, however, that there was a very great drain on the game fish population and that the increase of carp was rapid. Maskinonge fishing in Lake Simcoe has been negligible since 1910. The bass continued to be caught in fair numbers but decreased steadily until at present Lake Simcoe is no longer considered "good bass fishing." Under the lowered demands the present bass population may be expected to last for some time. The carp, from their introduction about 1896, increased so rapidly that in 1911, a catch of 462,000 lbs, was taken out without any effect being observed on their numbers.

In brief, the history of fishing in Lake Simcoe during the last sixty years may be summed up as follows. For forty years after 1868, there was a heavy drain on the game fish, bass and maskinonge and on the lake trout. During the last twenty-five years, the maskinonge have practically disappeared, bass have been much depleted and the carp is now the mainstay of the fishing.

FISH PRODUCTION IN LAKE SIMCOE

The amount of fish taken from a lake is not necessarily representative of its capacity for fish production any more than the crop from a poorly-tilled acre of land is representative of the possibilities of that acre. In agriculture we have fairly accurate data as to how much crop a given soil should produce, but in fish culture such a knowledge is as yet very scanty. In lieu of such information a comparison of the amount of fish taken from lakes of similar size may indicate

something of the relation of fish crop to possible productivity. In this connection, the fishery of Rainy lake, Ontario, may be compared with that of Lake Simcoe.

Rainy lake is situated on the boundary between Ontario and Minnesota. Its area of 324 square miles is comparable with that of Lake Simcoe. During the years of 1908-28, the average annual fishery from the Canadian waters, 267 square miles, of Rainy lake was 584,000 lbs. valued at $43,700.00. The composition of this catch has remained fairly constant, being composed of 29% pickerel, 24% pike, 17% whitefish, 16% ciscoes, and 14% mixed and coarse fish. Lake Simcoe, 280 square miles in area, yielded over the past sixty years an average fishery of 148,000 lbs., with an average value of $9,000. For equivalent areas the fishery in Rainy lake is 7.3 times as great and is worth 5.1 times as much as that of Lake Simcoe. It might be said that it is unfair to compare the catch in Lake Simcoe over sixty years with that in Rainy lake over twenty years. We should therefore consider the catch in Lake Simcoe, from 1880-1900, *i.e.*, twenty years at the first of its commercial fishing period, with the fish caught during the first twenty years of fishing in Rainy lake, *i.e.* 1908-28. During these two periods of twenty years, Rainy lake yielded 584,000 lbs. of fish per annum to 100,000 lbs. from Lake Simcoe, representing for equal areas a production of 5 to 1, the same ratio found in the former calculation. It must also be remembered that Rainy lake not only produced five times as much fish over a period of twenty years, but at the end of that time the fish fauna was apparently the same as at the beginning, while the smaller fishery in Lake Simcoe caused a depletion which still exists. The question arises as to whether this greater fish crop is due to the inherent productivity of the lake or to a better utilization of its possibilities.

The outline of Rainy lake is so irregular that the open-water areas are seldom more than four miles in width. The irregular shoreline has a length of about 790* miles, which, for a lake of 324 sq. miles in area, represents the enormous shore development of 12.4 (page 10). By including the shorelines of

*Measured from a map—scale 2 miles = 1 inch.

the numerous islands, the total reaches a length of 1,030 miles, a development of 16.1. The shoreline of Lake Simcoe is 144 miles (including islands), a shore development of only 2.27. A greater shore development indicates a greater proportion of protected bays, a heavier growth of aquatic vegetation and a correspondingly greater production of food organisms. The depth at Rainy lake is less than 15 metres over most of its area and the average depth is probably not more than 10 metres. From the depth and area relation, as stated on page 106, it is obvious that Rainy lake would be much more productive of bottom fauna than Lake Simcoe, both because of its lesser depth and its much greater shore development. It is conceivable that these physical advantages would enable Rainy lake to support an annual fishery worth $42,000, while Lake Simcoe is depleted by a fishery of $9,000. A second possibility has been mentioned above, that the productive capacity of Lake Simcoe may have been less efficiently utilized.

The shallow-water fish in Lake Simcoe, bass and carp have borne the brunt of the game and commercial fishing in the past twenty-five years. During this period the average annual catch of carp was about 68 tons. Over the same period, the average annual catch of trout was 7 tons and of whitefish 2.5 tons. It is obvious that the whitefish is the only desirable fish which utilizes the bottom food in deep water and that the trout is the only useful fish which, by feeding on the ciscoes, makes use of the plankton of the open water. If the carp and bass make use of the water down to a depth of 10 metres, and they rarely go so deep, there still remains a deep-water area of 200 square miles, 71% of the lake being deeper than 10 metres, from which less than ten tons of fish are taken annually. This 9.5 tons of trout and whitefish from 200 square miles of deep water is to be contrasted with 86 tons of carp and an unknown quantity of bass from the remaining 80 square miles. It would seem quite clear that a properly controlled gill net fishery for trout and whitefish would be an advantage in Lake Simcoe.

From the above data, it would seem probable that the

small quantity of fish taken from Lake Simcoe as compared with that taken from Rainy lake, is due both to the greater productivity of Rainy lake and to the incomplete utilization of the resources of Lake Simcoe.

FISH CULTURE IN LAKE SIMCOE

Fish culture in its widest and most useful sense is concerned as much with the utilization and conservation of the fish fauna as with the more widely recognized phase, that of rearing and planting fry or fingerlings. The present survey deals with only one phase of the conditions affecting fish life in a thorough manner. This phase, the food supply, is so fundamental in its effects that its investigation leads to a considerable understanding of the "fish condition" of the lake. The following discussion combines this understanding with observations on the limnology and the fish of the lake in an attempt to indicate what has been and may be done in fish culture in Lake Simcoe.

The Small-mouthed Black Bass

The early abundance of bass in Lake Simcoe is indicated by the average annual catch between the years 1868-1908 of $2,430, or 27% of the total fishery of the lake. At the present time a small number of bass is taken by anglers, their scarcity being demonstrated by the small numbers of anglers now attracted to the lake. This depletion, as has been suggested, is due both to the overfishing in former years and to the inroads of the carp, which appears to have crowded the bass off some of its former feeding and spawning grounds. The extent to which spawning has been interfered with is not known, although some of the better grounds have not been molested.

If restricted spawning is the factor that is suppressing the numbers of bass in Lake Simcoe, we might expect the introduction of fry to have beneficial effects. The following bass fry have been planted in Lake Simcoe:

1916	200,000
1917	100,000
1920	30,000
1921	25,000
1922	5,000
1923	5,000
1924	2,500
1926	500

While we have no means of estimating the result of this planting, it may be significant that many more bass were caught in 1928 than in any of eight years previous, while during the years preceding 1928 planting was at its lowest. Apparently the bass made some recovery of their own accord.

The value of bass fishing in Lake Simcoe is such that it deserves the best of protection. This protection is especially needed during the spawning period and throughout the twenty-day period after spawning, during the first days in which the eggs hatch and the young leave the nest and during the last days in which the male bass protects the young brood.

The Department of Game and Fisheries in 1927 advanced the open season for bass from June 15 to July 1. In 1928, observation of the bass at Beaverton indicated that on July 1 only a small proportion of the adult bass had spawned. This would seem to indicate that for some years at least, July 1st as the opening date is too early for the adequate protection of spawning and immature bass in Lake Simcoe.

The Carp

The rapid increase in numbers of carp following their introduction about 1896 has already been mentioned, as has the fact that carp make up 81% of the value of the present commercial fishery in the lake. Although the flesh of the carp is of a very inferior quality, the fishermen are able, by marketing them alive, to obtain as much as 10 or 12 cents per pound for their catch.

While the carp interfere little with the fish fauna of the deeper water it is a menace to the bass by crowding the latter off its feeding and spawning grounds. The relative values of

the present carp fishery, $8,100 annually, and the bass fishing, the value of which in attracting summer visitors is quite inestimable, is a difficult question. Should we decide that the bass were of more value than the carp, it is doubtful whether it would be possible to exterminate or greatly reduce the numbers of carp. Further, if the carp could be reduced in numbers, it is again doubtful whether the bass fishing could be restored to what it was prior to the inroads of the carp. Due to the fact that it is impossible to seine in much of the grounds inhabited by carp, it is unlikely that it could ever be satisfactorily kept down, although allowing the fishermen to take it during the spawning season would tend to reduce its numbers to some extent. Such a policy could not be recommended at present in view of the doubt as to the possible restoration of the bass.

The carp interfere with the other fishes of the shallow water by stirring up the bottom mud and uprooting the aquatic vegetation. They have destroyed completely the wild-rice beds in Cook's bay and several recent attempts to re-introduce this plant have been frustrated by the rooting tendencies of the carp.

The Lake Trout

While the opinion of residents on the lake is that the trout are very much depleted, experimental gill net settings indicate that they are still present in moderate numbers. The impression of scarcity is derived from the difficulty with which trout are taken on a troll or by spearing through the ice. It is thought that this difficulty is due in part to the moderate numbers of fish and in part to the abundance of their food supply. The number of ciscoes taken from the stomachs of trout supports the latter view. It has been suggested that the moderate population of trout is due to some condition which interferes with the production and development of the young trout up to a size at which they can begin to feed upon the cisco. Although this theory appears to be quite plausible, it cannot be tested till the life-history of the lake trout has been worked out.

In view of the fair numbers of adult trout and the very numerous and suitable spawning grounds, it is doubtful whether stocking with fry is to be recommended. During the past ten years some 2,110,000 lake trout fry have been planted in Lake Simcoe, mostly along the shores. In at least two cases, the fry were "dumped" off the dock and numerous perch were observed to have eaten a large percentage of them in a short time.

The Whitefish

The whitefish are still abundant in the lake and the fishermen turn to them when they find the trout too difficult to capture. The small size attained by whitefish in Lake Simcoe is remarkable, the average weight of adult fish being only 1 lb. 2 oz. Since the larger whitefish in our Great lakes and in Lake Nipigon depend in part on the amphipod, *Pontoporeia hoyi*, for food, the absence of this species in Lake Simcoe may have some effect in limiting the size of the whitefish. It is thought more probable that the small size is due to an overcrowding and a resultant competition for food. Such condition is said to be responsible for the small size of perch in many lakes where that species is numerous (Dymond, 1926). In view of this small average weight it is obvious that the minimum weight limit for whitefish in Lake Simcoe should be not more than one pound instead of the two pound limit as enforced in the Great Lakes.

The present annual catch of 2.5 tons of whitefish is almost negligible when one considers the large area of deep water in Lake Simcoe. It is suggested that a limited amount of gill netting for whitefish in Lake Simcoe would be an advantage in increasing the fish crop of the lake, by removing some of the suckers and ling and possibly by allowing the whitefish, with less competition, to reach a larger average size.

The Pickerel

In the years 1921-24, a total of 2,400,000 pickerel fry were planted in Lake Simcoe, the largest lot being 1,000,000

introduced in 1924. This action seems hardly justified in view of the fact that the few pickerel which occurred naturally in the lake some fifteen years ago failed to thrive. Moreover, there is no barrier to prevent the pickerel from Lake Couchiching entering Lake Simcoe should they find the latter a suitable habitat. Apparently none of the fry introduced have been seen since although they have had plenty of time to reach maturity.

THE MASKINONGE

The maskinonge (lunge), abundant thirty years ago, is at present very scarce in the lake, being practically confined to the Holland river and the lower end of Cook's bay. It is doubtful whether this fish could ever be re-established in the lake under present conditions.

THE RAINBOW TROUT

The scattered specimens of the rainbow trout taken near Orillia may be regarded as indicating that at least a few of the fry of this species, planted in the lake, were able to reach maturity. In view of its fine game qualities, a characteristic quite lacking in the larger lake trout, it would seem advisable to make an attempt to establish this or a closely related species in Lake Simcoe.

SUMMARY OF PART III

As a result of the above considerations, the following conclusions have been reached with regard to the fisheries of Lake Simcoe:

1. In the early years, 1868-1908, the game fish, bass and maskinonge, were greatly overfished in Lake Simcoe.

2. This overfishing, combined with the introduction of carp, 1896, has resulted in an almost complete destruction of the maskinonge and a great depletion of the bass.

3. During the last twenty years, the carp has provided 81% of the value of the average annual catch and in doing so

has made up in quantity only for the damage it has caused to fishing in the lake.

4. While Lake Simcoe is undoubtedly less productive of fish and fish food than some other lakes of similar area, a second reason for the small annual catch is the failure to utilize the fish supported by the deep water areas.

5. Both the public and the lake itself would benefit by a limited gill-net fishing for whitefish and trout.

6. The planting of most species, especially in the fry stage, in Lake Simcoe is probably not justified, a possible exception being the rainbow trout, which might be a desirable addition to the present fish fauna.

General Summary

The subject has been treated in three parts. *Part I* deals with the bottom fauna, its composition, distribution and quantity as well as the factors responsible for this composition, distribution and quantity. *Part II* is a discussion of the position of bottom fauna in the ecology of the lake and an application of our knowledge of bottom fauna to some of the problems of nutriment or food circulation in lakes. *Part III* includes certain data as to the fisheries of the lake and combines these data with the results of the bottom fauna survey in explaining the past depletion of the fish fauna in Lake Simcoe and in making certain suggestions as to the future of fish culture in Lake Simcoe.

The results and conclusions of each aspect of the investigation have been summarized at the end of each part on pages 117, 153 and 174, respectively.

The substance of the paper may be suggested as follows:

Lake Simcoe is 280 sq. miles in area and has an average depth of 17m. (54 ft.). Its shores are much exposed, due to the broad expanse of open water, and its water is clear, cool and slightly alkaline. A marked thermal stratification occurs in the lake at midsummer with a resultant lowering of the oxygen supply in deep water.

The bottom fauna of the lake comprises a large number of species and groups, the shallow water supporting a much more varied fauna than the deep water. The fauna of deep water in Lake Simcoe is composed of a larger number of species than that of small, more completely stratified lakes, probably due to the oxygen content which, though scanty, is never completely lacking in Lake Simcoe.

The intermediate size, exposure to water movements and the small quantity of oxygen in the deep water are the factors which are chiefly responsible for the nature of bottom fauna in Lake Simcoe and for the differences between its fauna and that of other lakes. The fairly rich bottom fauna and plankton, the low oxygen content of deep water, indicate that Lake Simcoe is an eutrophic lake. The distribution of the bottom fauna as compared with that of typical European eutrophic lakes substantiates this conclusion.

The quantity of bottom fauna over all depths in Lake Simcoe is 12.38 kgm. dry weight per hectare exclusive of mollusc shells. Chironomid larvae make up 65 per cent. of this quantity, Mollusca 18 per cent., and the remainder is composed of ephemerid nymphs, Amphipoda, Oligochaeta and *Corethra* larvae. It has been shown that lakes usually possess a quantity of bottom fauna which is proportional to the product of their depth and area, and that the quantity of bottom fauna in Lake Simcoe is as great as would be expected in a lake of this size. It has been estimated that the annual production of bottom fauna in Lake Simcoe is approximately 30 kgm/ha dry weight as compared with the average fauna of 13.38 kgm/ha throughout the months May to October.

The circulation of food in a lake is a very complex series of cycles, a suggestion of which is given in diagram 3 (page 122). The amount of nutritive material in the form of living plankton and bottom organisms is very small, perhaps 0.5 per cent., as compared to the amount of nitrogeneous organic material dissolved in the water and present in the upper 5 cm. of the bottom ooze. The rate of circulation of nutritive materials depends on a large number of factors, among which

the trophic condition of the lake, the temperature and the length of the growing season are very important. The utilization of successive forms of food material varies greatly in different lakes, resulting in what has been termed a "disharmony of production." The quantity and quality of bottom fauna in a lake is to some extent indicative of the richness or the amount of nutritive material in circulation, but it should be used in combination with other indices.

Fishing in Lake Simcoe has had an unusual history during the past sixty years. During the first forty years the game fish were greatly exploited. Of the annual catch of 55,000 lb., valued at $9,000.00, bass and maskinonge made up 46 per cent. During the last twenty years the annual catch of 234,000 lb., valued at $10,000.00, has been chiefly composed of coarse fish, 81 per cent. carp. Overfishing in the early years and the introduction of carp about 1896, have completely destroyed the maskinonge fishing and depleted the bass and trout to a considerable extent. The present small catch of fish is due in part to a failure to utilize the fish of the deep water so that a limited gill-net fishing for whitefish and trout has been recommended. Planting of fry in the lake is not recommended with the possible exception of the rainbow trout.

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PLATE I.

Fig. 1. Ekman dredge open.

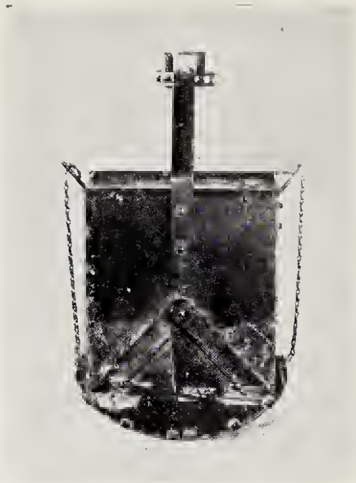

Fig. 2. Ekman dredge closed.

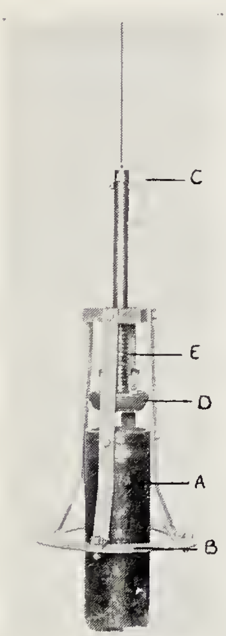

Fig. 3. Heavy sampler "set."

Fig. 5. Shell for sampler.

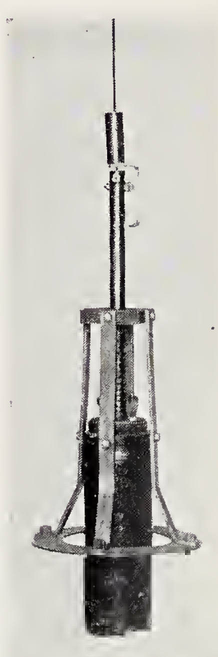

Fig. 4. Heavy sampler released.

Plate II.

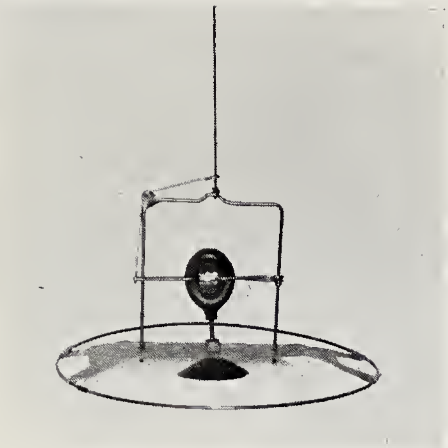

Fig. 1. Ooze sucker "set."

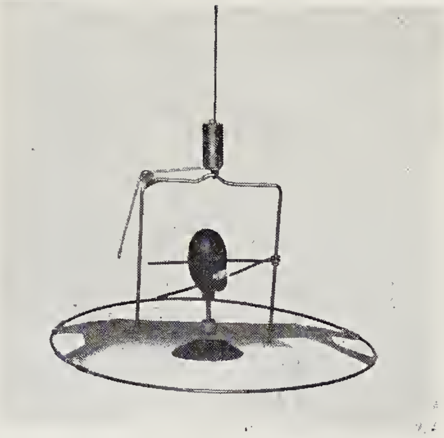

Fig. 2. Ooze sucker released.

Fig. 3. Funnel and bulb of ooze sucker.

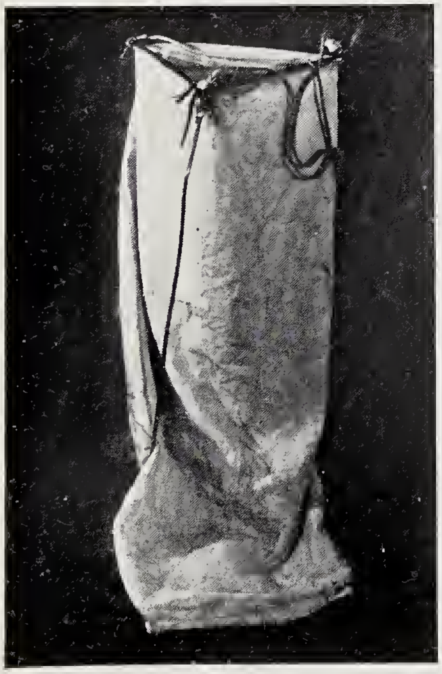

Fig. 4. Triangular mouth tow net.

Fig. 5. Bottom net with sheath folded up.

Plate III.

Portion of exposed rocky shore of Lake Simcoe.

Plate IV

Fig. 1.—Fishing for ciscoes on the bay at Atherley, July 1, 1928.

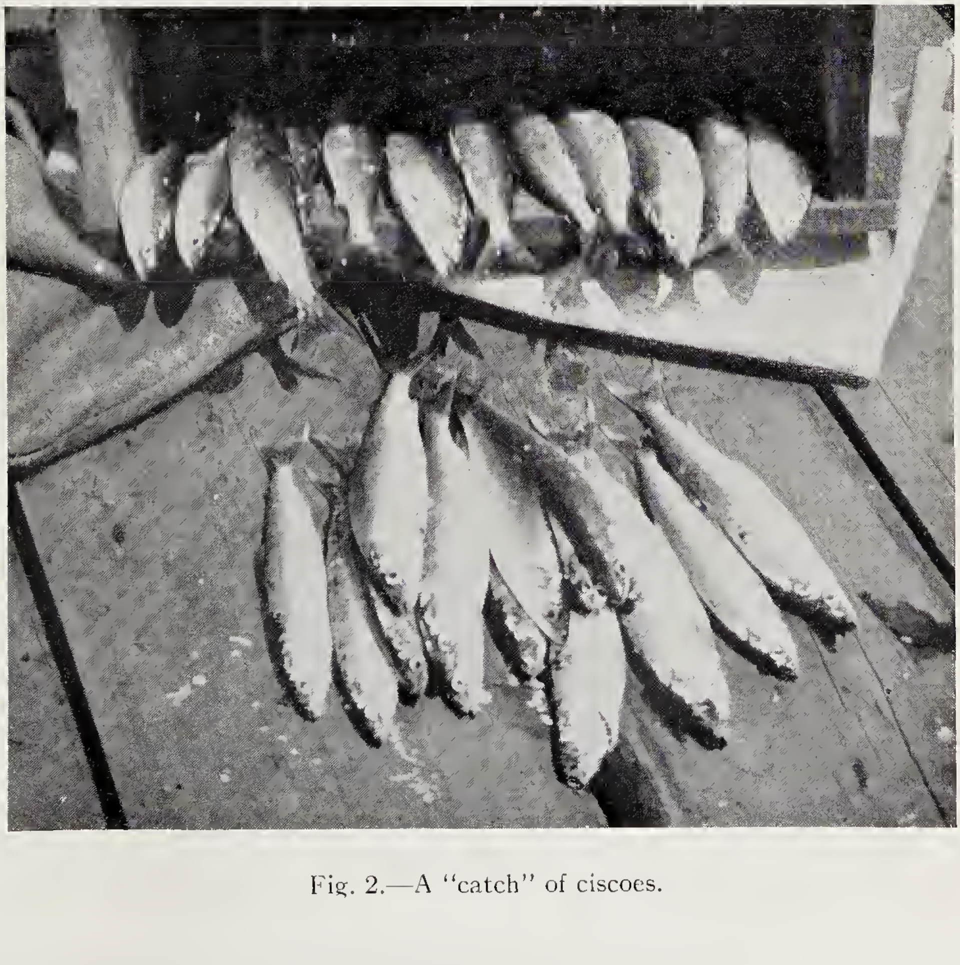

Fig. 2.—A "catch" of ciscoes.

PLATE V

Fig. 1.—A fish-house used for fishing through the ice.

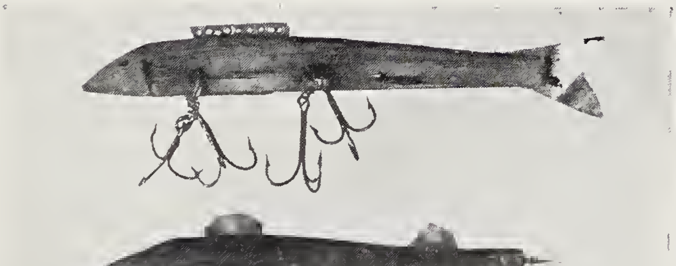

Fig. 2.—Home-made decoys used for trout fishing.

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